Lower Turonian (Cretaceous) ammonites from south-east Nigeria

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Synopsis

Within most of Nigeria's Benue Trough uppermost Cenomanian and Lower Turonian strata are dominated by vascoceratid ammonite faunas of Tethyan affinities. Such assemblages range as far south as the Ezillo region in south-east Nigeria where *Nigericeras*, *Paravascoceras*, *Fagesia*, *Thomasites* and *Wrighto-*

ceras occur. Barely 60 km south, however, at Lokpanta, the Lower Turonian contains faunas more easily correlated with those of the western interior of the United States and north-west Europe. The basal Turonian here is mainly characterized by *Watinoceras* spp., while the upper part of the Lower Turonian contains *Pachydesmoceras*, *Mammites nodosoides* (Schlüter), *Kamerunoceras*, *Fagesia*, *Neoptychites*, *Herrickiceras*? and *Hoplitoides latefundatus* sp. nov. This last form appears to provide an evolutionary link between *Wrightoceras* and typical *Hoplitoides*. The absence of the vascoceratid-rich faunas at Lokpanta is probably because of palaeoenvironmental factors.

Introduction

Uppermost Cenomanian and Turonian sediments are among the most widely distributed and richly fossiliferous parts of the Cretaceous system in Nigeria. During the early phases of systematic palaeontological work in Nigeria diverse collections of ammonites were attributed to the Lower Turonian (Reyment 1954, 1954*a*, 1955, 1957, Barber 1957). In recent years,

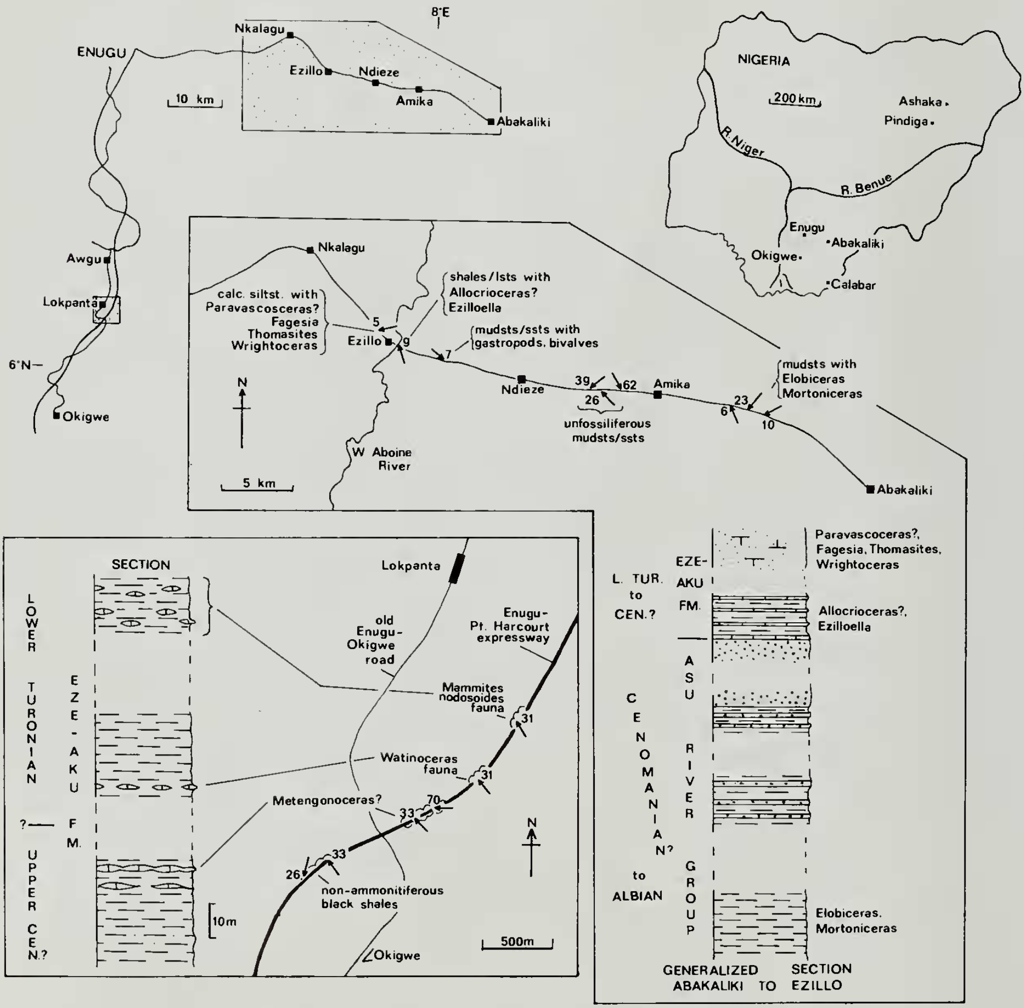


Fig. 1 Maps showing fossil localities and sections described in the text.

however, much of this material has been reassigned to the Upper Cenomanian and Middle Turonian. As a consequence, the faunal character of the Lower Turonian and its correlation within and outside Nigeria are in need of clarification. Material from the Lower Turonian of south-eastern Nigeria described here makes a considerable contribution to this.

The present faunas come from two areas (see Fig. 1). On the western outskirts of Ezillo (Eze-ilo), adjacent to the Enugu–Abakaliki highway, a disused pit exposes gently-dipping, micaceous, calcite-cemented siltstones yielding *Thomasites gongilensis* (Woods), *T. koulabicus* (Kler), *Wrightoceras wallsi* Reyment, *W.* cf. *munieri* (Pervinquière), *Fagesia* sp. and *Paravascoceras*? sp. Immediately south of Lokpanta three cuttings are present in a distance of less than 1 km on the Enugu–Port Harcourt expressway. In the most northerly of these cuttings 10–12 m of black, weathering sandy yellow, shales with large calcareous nodules contain an ammonite fauna of *Pachydesmoceras denisonianum* (Stoliczka), *Kamerunoceras puebloense* (Cobban & Scott), *Mammites nodosoides* (Schlüter), *Neoptychites cephalotus* (Courtiller), *Fagesia levis* Renz, *Hoplitoides latefundatus* sp. nov. and *Herrickiceras*? sp. Although ammonites occur here in their hundreds, larger specimens are, almost without exception, so badly crushed as to be unidentifiable. It is therefore usually the juvenile and middle whorls alone that are suitable for description. Directly south, a second cutting displays about 25 m of the closely similar underlying shales. In the lower 5 m of this sequence there are bands of dark grey, weathering sandy yellow, calcareous nodules whose surfaces are studded with the impressions of *Watinoceras* aff. *amudariense* (Arkhanguelsky), *W.* sp., *Kamerunoceras* cf. *eschii* (Solger), *Mammites*? sp. and *Neoptychites cephalotus*. Only tiny ammonites are preserved complete, the larger forms being recognized by fragments. The most southerly cutting exposes over 40 m of shales, silty in places, which include thin calcareous horizons formed from coalesced nodules. These beds are less fossiliferous but from their upper part have yielded several poorly preserved impressions of *Metengonoceras*? (Fig. 9, p. 39). The regional dip in these cuttings averages a little over 30° north-west, but rises abruptly to 70° west at the northern end of the last-described exposure. This fact suggests the proximity of faulting, and indeed minor faults can be observed within these cuttings.

The shales, silts and calcareous beds of late Cenomanian? to early Turonian age in most parts of southern Nigeria are conventionally referred to as the Eze-Aku Formation. This lithostratigraphic unit, formalized by Simpson (1954), is, however, not readily distinguishable from superjacent beds and is recognized primarily on the basis of its age. Though this is contrary to accepted stratigraphical practice, it is outside the scope of the present work to adopt other than a traditional approach here. A fuller discussion can be found in Petters & Ekweozor (1982).

Systematic descriptions

Repositories. Register numbers prefixed by the letter C are of specimens in the Department of Palaeontology, British Museum (Natural History), London. Those prefixed by the abbreviation UIN are of specimens in the Department of Geology, University of Ilorin, Nigeria.

Dimensions (in mm). D, diameter; Wb, whorl breadth; Wh, whorl height; U, umbilical diameter. Figures in parentheses are dimensions as a percentage of the total diameter. N = number of ribs in last whorl.

Superfamily **DESMOCERATACEAE** Zittel, 1895

Family **DESMOCERATIDAE** Zittel, 1895

Subfamily **PUZOSIINAE** Spath, 1922

Genus ***PACHYDESMOCERAS*** Spath, 1922

TYPE SPECIES. *Ammonites denisonianus* Stoliczka, 1895; by original designation.

Pachydesmoceras denisonianum (Stoliczka, 1865)
Figs 2–4

1865 *Ammonites denisonianus* Stoliczka: 133 (*pars*); pl. 66, fig. 2 (only); pl. 66a (*non* pl. 65, fig. 4; pl. 66, fig. 1).
1898 *Puzosia Denisoniana* (Stoliczka) Kossmat: 121; pl. 14, figs 5a, 5b; pl. 15, figs 5a, 5b.
1898 *Desmoceras Kamerunense* von Koenen: 55; pl. 7, figs 1–3.
1899 *Puzosia alimanestianui* Popovici-Hatzeg: 14; pl. 1.
1904 *Puzosia Denisoniana* (Stoliczka); Solger: 103; pl. 3, figs 1a, 1b; text-fig. 5.
?1904 *Puzosia Denisoni* (Stoliczka); Douvillé: 237; pl. 29, figs 1–4; pl. 30, figs 1a, 1b.
1907 *Desmoceras* (*Puzosia*) *Denisonianum* (Stoliczka) Boule, Lemoine & Thévenin: 21; pl. 5, figs 3–5.
?1912 *Puzosia denisoniana* (Stoliczka); Zimmermann: 542; pl. 26.
1914 *Puzosia denisoniana* (Stoliczka); Yabe: 72; pl. 7
1922 *Pachydesmoceras denisonianum* (Stoliczka) Spath: 127
1954 *Pachydesmoceras denisonianum* (Stoliczka); Matsumoto: 100 (with synonymy).
1955 *Pachydesmoceras kamerunense* (von Koenen); Reyment: 19.
1958 *Pachydesmoceras denisonianum* (Stoliczka); Reyment: 54.
1961 *Pachydesmoceras denisoni* (Stoliczka); Collignon: 39; pl. 8, figs 1a, 1b.
1965*a* *Pachydesmoceras denisoni* (Stoliczka); Collignon: 22; pl. 422, fig. 1752.

MATERIAL AND OCCURRENCE. Fourteen specimens (C.83511, C.85290–2, C.90292–301) from the Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria.

DIMENSIONS.	D	Wb	Wh	U
C.90298	36	12·5 (35)	17 (47)	9 (25)
C.90297	50	15 (30)	22 (44)	13 (26)
C.90294	60	23 (38)	28 (47)	17 (28)
C.90292	65	25 (38)	29 (47)	18 (28)
C.90293	71	27 (38)	35 (49)	19 (27)

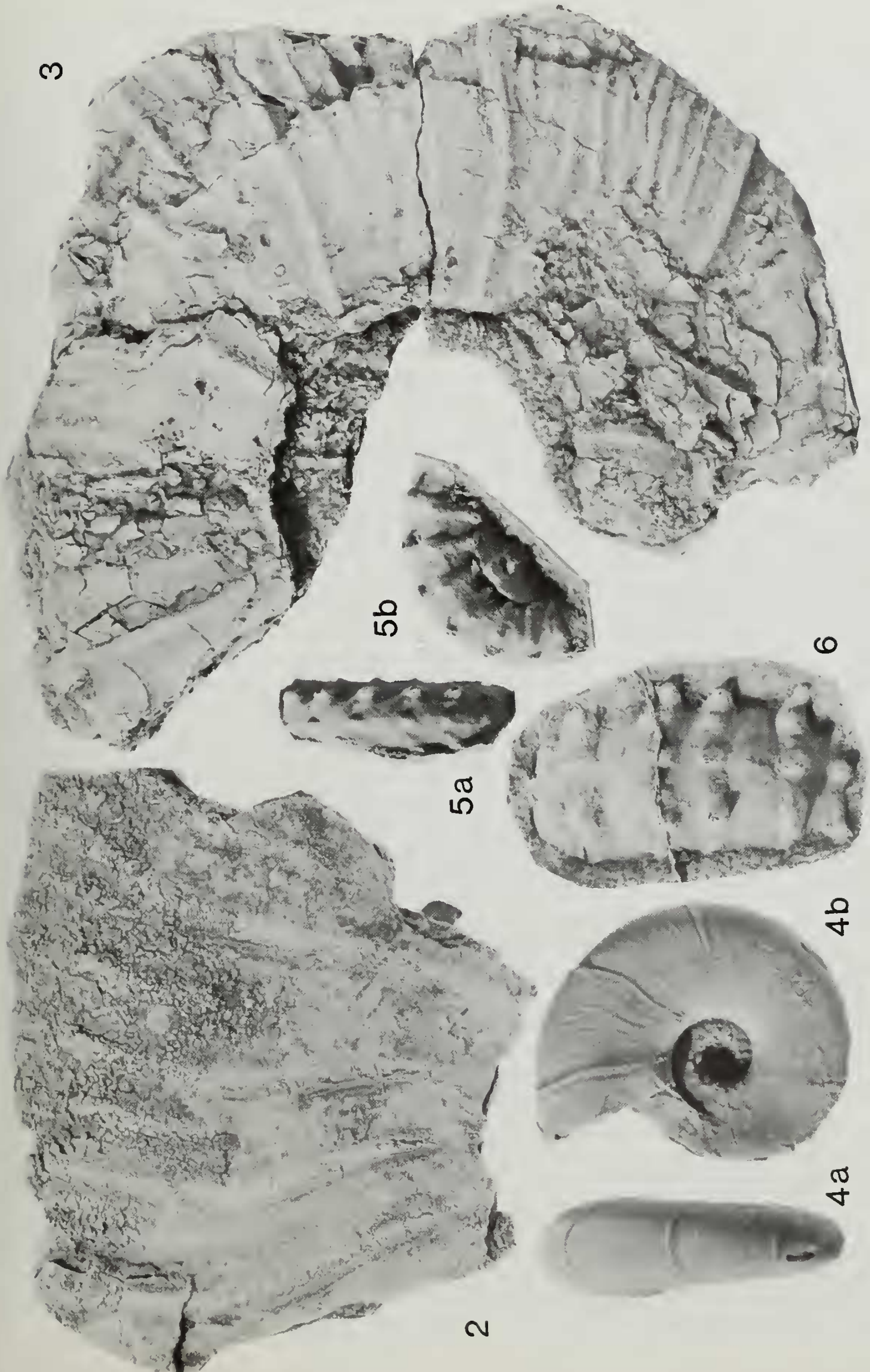
DESCRIPTION. The shell is moderately evolute, moderately compressed and has a broadly rounded venter. The earliest whorls are smooth but at diameters of 15–20 mm faint, narrow ribs appear in the ventral area. These ribs gradually extend to the umbilical shoulder, there being about eight in each whorl. At diameters of 40–50 mm minor ribs appear, confined to the outer part of the flank and the venter. They gradually strengthen and in the middle stages may outnumber the major ribs by as many as ten to one. In the later stages the major ribs dominate and at diameters in excess of 150 mm there are only one or two minor ribs intervening.

REMARKS. This material is exactly comparable with that described from Cameroun by Solger (1904: 103; pl. 3, figs 1a, 1b; text-fig. 5) as *Pachydesmoceras denisonianum* (Stoliczka). Reyment (1955: 17) at first included Solger's specimens in *P. kamerunense* (von Koenen), differentiating it from *P. denisonianum* on the basis of minor ribbing details and degree of inflation. Later, however, Reyment (1958: 54) referred them back to the latter species. There do not seem to be any significant differences between the Nigerian/Camerounian material and *P. denisonianum* and they are treated here as conspecific. *Puzosia alimanestianui* Popovici-Hatzeg (1899: 14; pl. 1) is another probable synonym. The inner whorls in the holotype of *P. hourcqi* Collignon (1961: 42; pl. 11, fig. 1) are poorly preserved but its later ornament resembles that in the present material and it may also be conspecific.

P. denisonianum and indistinguishable forms have a long stratigraphical range, at least from Cenomanian to Coniacian. *P. pachydiscoides* Matsumoto (1954: 101; pl. 9, figs 2a, 2b) is said to

Figs 2–4 *Pachydesmoceras denisonianum* (Stoliczka). Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Fig. 2, C.85290, × 1. Fig. 3, C.90301, × 1. Fig. 4a, b, C.90297, × 1.

Figs 5–6 *Kamerunoceras* cf. *eschii* (Solger). Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria. Fig. 5a, b, C.90370, × 1·5. Fig. 6, C.90371, × 1. Both latex casts.


3
5b
6
5a
4b
4a
2

have higher whorls and more projected ribs than *P. denisonanum*. *P. maroccanum* Collignon (1966: 26; pl. 12, fig. 4) has broader whorls and develops strong ribbing earlier. In *P.*(?) *linderi* (Grossouvre 1894: 188; pl. 24, fig. 4; Collignon 1961: 41; pl. 10, figs 1, 1a; 1965: 8; pl. 379, fig. 1640) all ribs are of equal strength in the earlier whorls. *P. radaodyi* Collignon (1964: 58; pl. 333, fig. 1498) and *P. rarecostatum* Collignon (1961: 40; pl. 9, figs 1, 1a) both have stronger major ribbing which dominates the ornament even in the middle growth stages.

Superfamily **ACANTHOCERATACEAE** Grossouvre, 1894

Family **ACANTHOCERATIDAE** Grossouvre, 1894

Subfamily **EUOMPHALOCERATINAE** Cooper, 1978

Genus ***KAMERUNOCERAS*** Reyment, 1954*a*

TYPE SPECIES. *Acanthoceras eschii* Solger, 1904; by original destination.

Kamerunoceras cf. ***eschii*** (Solger, 1904)
Figs 5–6

cf. 1904 *Acanthoceras eschii* Solger: 124; pl. 4, figs 1–4.
non 1954*a* *Kamerunoceras eschii* (Solger) Reyment: 251; pl. 3, fig. 5; pl. 5, figs 3, 6; text-figs 2a, 2b (= *Kamerunoceras seitzi* (Riedel)).
non 1955 *Kamerunoceras eschii* (Solger); Reyment: 59 (= *Kamerunoceras seitzi* (Riedel)).
cf. 1958 *Kamerunoceras eschii* (Solger); Reyment: 55; pl. 1, figs 1a, 1b; pl. 2, figs 1a, 1b.
cf. 1979 *Kamerunoceras eschii* (Solger); Kennedy & Wright: 1166, 1175–1176; pl. 1, figs 4–9.

MATERIAL AND OCCURRENCE. Two specimens (C.90370–1) from the Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria.

DESCRIPTION. The smaller of these two specimens (C.90370, Fig. 5a, b) has a diameter of about 25 mm. It is evolute, its whorl breadth and whorl height being approximately equal. There are 16–17 ribs per whorl which are prominent only on the flanks where each bears bullate umbilical and inner ventrolateral tubercles. The ribs are effaced upon the venter where the ornament consists of clavate outer ventrolateral and siphonal tubercles, the latter situated a little adoral of the former. There are no minor ribs. The larger specimen (C.90371, Fig. 6) has a whorl breadth of some 20 mm. Again ribbing dominates the flank ornament while tubercles are more prominent upon the venter. There are strong, moderately spinose inner ventrolateral and weaker outer ventrolateral tubercles fusing to form a bituberculate structure. Along the median line are strong, rounded siphonal tubercles. Rib spacing is irregular. Minor ribs are absent.

REMARKS. Of the multitude of species referred to *Kamerunoceras* (see list in Kennedy & Wright, 1979), the present material is closest to the type species *K. eschii* (Solger 1904: 124; pl. 4, figs 1–4; Reyment 1958: 55; pl. 1, fig. 1; pl. 2, fig. 1; Kennedy & Wright 1979: 1175–1176; pl. 1, figs 4–9). Unfortunately, this is a poorly understood form, known only from the imperfectly preserved type specimen from southern Cameroun. It agrees, however, in its rather broad whorls, prominent flank ribs and comparatively massive ventrolateral tuberculation.

Kamerunoceras puebloense (Cobban & Scott, 1972)
Figs 7–8

1972 *Kanabiceras puebloense* Cobban & Scott: 73; pl. 15, figs 8, 9; pl. 37, figs 1–8; pl. 38, fig. 1.
1979 *Kamerunoceras puebloense* (Cobban & Scott) Kennedy & Wright: 1170.

MATERIAL AND OCCURRENCE. Four specimens (C.83518, C.90342–4) from the Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Two further specimens (C.85299–300) from the same horizon and locality may also belong here.

DESCRIPTION. The shell is evolute with pentagonal whorl sections, which are a little higher than broad in the early stages, but slightly broader than high later on. Between diameters of 15 and

25 mm there are numerous ribs of markedly uneven development. These are projected forwards on the flank, backwards over the ventrolateral shoulder and form distinct chevrons over the venter. Major ribs bear prominent and spinose umbilical, inner and outer ventrolateral tubercles and more subdued but still well-defined siphonal tubercles. There are numerous intercalated ribs lacking umbilical tubercles but sometimes bearing subdued ventrolateral and siphonal tubercles; others show virtually no tubercle development at all. The venter is crossed by deep, chevron-shaped constrictions. At diameters of 50–70 mm the ribbing becomes more rectiradiate and regular, constrictions disappear and the major ribs come to dominate the ornament. Each bears highly spinose umbilical, inner and outer ventrolateral tubercles and a slightly lower siphonal tubercle. Intercalated ribs, dying out in the mid-flank region, generally alternate with the major ribs. They usually show exactly the same style and strength of ventral tuberculation as do the latter though the inner ventrolateral tubercles may be effaced. At these diameters there occur only a very few additional weak, fold-like ribs lacking tubercles altogether.

REMARKS. Cobban & Scott (1972: 73) first described *Kamerunoceras puebloense* from the Lower Turonian (*Mammites nodosoides* Zone) of Colorado. They referred it to *Kanabiceras* Reeside, a genus shown by Kennedy *et al.* (1981: 55) and Wright & Kennedy (1981: 54–55) to be a synonym of *Euomphaloceras* Spath. In fact, as pointed out by Wright & Kennedy (1981: 56), this species combines juvenile ornamentation similar to that in late members of *Euomphaloceras* with the evolute coiling and adult ornament characteristic of *Kamerunoceras*. Thus the early constriction-bearing whorls with their much multiplied, chevron-forming ventral ribs and tubercles resemble those in the late Cenomanian *Euomphaloceras euomphalum* (Sharpe) (see Kennedy 1971: 91; pl. 43, fig. 1; pl. 59, figs 1–5; Wright & Kennedy 1981: pl. 11, figs 1–8) and *E. septemseriatum* (Cragin) (see, for example, Cobban & Scott 1972: pl. 12, figs 5–27; Wright & Kennedy 1981: pl. 12, figs 1–8; pl. 13, figs 1–6; pl. 14, figs 5–9). Conversely, the evolute coiling and adult whorls with their lesser secondary ornament and more rectiradiate ribbing show closer similarities to *Kamerunoceras* (see Kennedy & Wright 1979 for a review of this genus). Since this material is clearly trending towards *Kamerunoceras* it is included therein, following the suggestions of Cooper (1978: 110), Kennedy & Wright (1979: 1170) and Wright & Kennedy (1981: 56). Although *K. puebloense* forms a clear link between its genus and the presumably ancestral *Euomphaloceras*, the more typical *Kamerunoceras*, *K.* cf. *eschii*, occurs below it at Lokpanta. As in Nigeria, *K. puebloense* is found in the upper part of the Lower Turonian in Colorado, though a similar form has been described from the very late Cenomanian of southern England (Wright & Kennedy 1981: 56; pl. 14, figs 3, 11).

The later whorls of *K. schindewolfi* (Collignon 1965: 31; pl. 389, fig. 1665) resemble those in the present material in their spinose tubercles and persistent minor ribbing. There are, however, mid-lateral tubercles in *K. schindewolfi*.

Subfamily **MAMMITINAE** Hyatt, 1900

Genus ***WATINOCERAS*** Warren, 1930

TYPE SPECIES. *Watinoceras reesidei* Warren, 1930 (= *Acanthoceras amudariense* Arkhanguelsky, 1916); by monotypy.

Watinoceras aff. ***amudariense*** (Arkhanguelsky, 1916)
Figs 10–12

MATERIAL AND OCCURRENCE. Three specimens (C.90366–8) from the Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria.

DIMENSIONS.	D	Wb	Wh	U	N
C.90367	13	4·5 (35)	5·6 (43)	3·8 (29)	37
C.90366	9	—	3·8 (42)	3·1 (34)	42

DESCRIPTION. The material at hand is of small size, the largest specimen having a diameter of only 13 mm. The shell is moderately evolute, compressed, with flattened flanks and, at first, a rounded venter, the whorl section becoming more pentagonal in shape later. The whorls are smooth up to diameters of 3–4 mm, when ribs appear, at first confined to the outer part of the flank and the venter. The whorls thereafter bear dense, rounded ribs mostly arising in pairs at the umbilical shoulder but sometimes bifurcating some distance down the flank. Intercalated ribs also occur. The ribs are projected over the venter but are interrupted by a narrow ventral sulcus. There are weak ventrolateral tubercles but umbilical tubercles become noticeable only at the largest diameters seen. One specimen (C.90368, Fig. 12), 11 mm in diameter, shows somewhat coarser ribs than the other two on its outer whorl. They form prominent chevrons upon the venter where they are again interrupted by a narrow sulcus.

REMARKS. Owing to their extremely small size, it is not possible to assign these specimens definite specific status. They most closely resemble the inner whorls of *Watinoceras amudariense* (Arkhanguelsky 1916: 48; pl. 7, figs 8–13; Wright & Kennedy 1981: 51; pl. 10, figs 6, 14; text-figs 19N, 19Q (with synonymy)), of which *W. reesidei* Warren (1930: 67; pl. 3, fig. 2; pl. 4, figs 9–12; see also, for example, Cobban & Gryc 1961: 186; pl. 38, figs 46–49) is the main synonym. The Nigerian material has a similar rib density and style of ornament, and such range as it shows in these features falls within that exhibited by figured specimens of this species. Thus the most coarsely ribbed Nigerian variant (C.90368) is similar to the example figured by Arkhanguelsky (1916: pl. 7, fig. 9). The main difference shown by the present material is its rather smaller umbilical diameter, 29–34% of the overall diameter against a consistent figure of about 40% in *W. amudariense*. In this respect the former is closer to specimens from Tarfaya figured by Collignon (1966: pl. 19, figs 14, 15) as *W.* sp. aff. *reesidei* Warren.

Watinoceras sp.
Figs 13–17

MATERIAL AND OCCURRENCE. Seven specimens (C.90361–5a, b, C.90369) from the Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria.

DIMENSIONS.	D	Wb	Wh	U	N
C.90365a	9	3·3 (37)	3·3 (37)	2·8 (31)	33
C.90365b	9·5	—	4·3 (45)	2·6 (27)	25
C.90369	12·5	6·5 (52)	4·5 (36)	3·6 (29)	27
C.90363	14	—	6 (43)	4 (29)	26

DESCRIPTION. This material is again of small size, the largest specimen having a diameter of 14 mm. The shell is moderately evolute. Its whorl height and whorl breadth are approximately equal at a diameter of about 9 mm but the latter increases much more rapidly so that the whorls develop a markedly depressed, pentagonal shape later on. The shell is smooth until

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Figs 7–8 *Kamerunoceras puebloense* (Cobban & Scott). Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Fig. 7a, b, C.90342, × 1. Fig. 8a–c, C.90344, × 1.

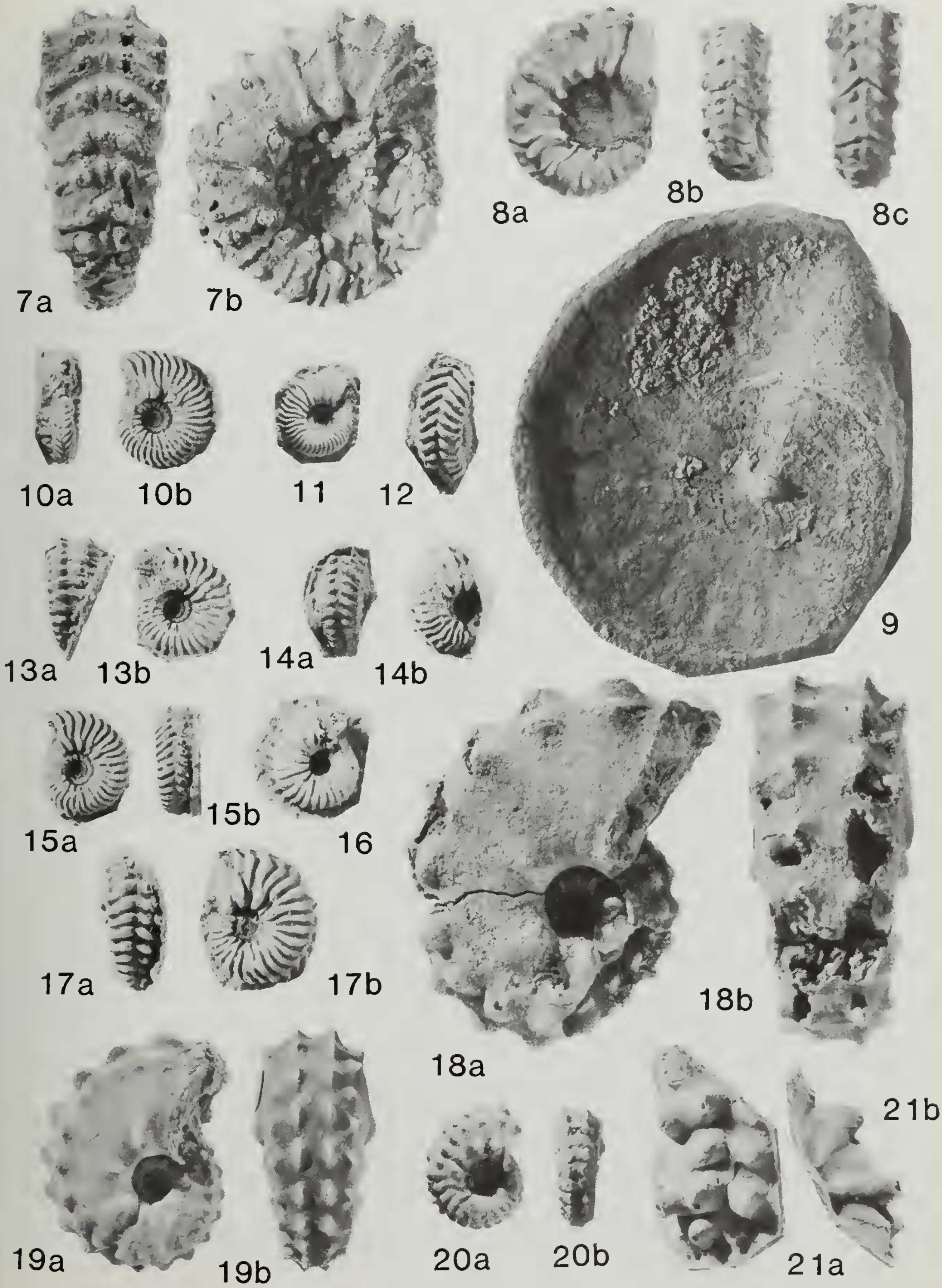
Fig. 9 *Metengonoceras*? sp. Eze-Aku Formation (Upper Cenomanian?), Lokpanta, south-east Nigeria. C.90373, × 1. This specimen shows pseudoceratitic sutures.

Figs 10–12 *Watinoceras* aff. *amudariense* (Arkhanguelsky). Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria. Fig. 10a, b, C.90367, × 1·5. Fig. 11, C.90366, × 1·5. Fig. 12, C.90368, × 1·5. All latex casts.

Figs 13–17 *Watinoceras* sp. Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria. Fig. 13a, b, C.90369, × 1·5. Fig. 14a, b, C.90362, × 1·5. Fig. 15a, b, C.90365a, × 2. Fig. 16, C.90365b, × 1·5. Fig. 17a, b, C.90363, × 1·5. All latex casts.

Figs 18–20 *Mammites nodosoides* (Schlüter). Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Fig. 18a, b, C.90336, × 1. Fig. 19a, b, C.90337, × 1. Fig. 20a, b, C.90341, × 1·5. See also Fig. 22a, b.

Fig. 21a, b *Mammites*? sp. Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria. C.90360, × 1·5. Latex cast.


7a
7b
8a
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21b

diameters as large as 4 mm, when fairly dense, rounded ribs appear. Prominent tubercles arise at a very early ontogenetic stage, the outer ventrolateral tubercles developing first, followed by the inner ventrolateral and umbilical tubercles. By a diameter of 10 mm all the tubercle rows are prominent and spinose. As growth proceeds rib density is reduced, the ribs themselves becoming higher and sharper. They mostly arise in pairs from the umbilical tubercles, though some intercalatories are also present. The ribs are projected forwards over the ventrolateral shoulders but are interrupted along the median line by an increasingly broad ventral sulcus.

REMARKS. The main characteristics of this form are its great whorl breadth and strong ornament. No previously described *Watinoceras* shows such a depressed whorl section at comparable diameters. *W. devonense* Wright & Kennedy (1981: 52; pl. 10, figs 7, 10, 12?, 13, 16) and *W. coloradoense praecursor* Wright & Kennedy (1981: 52; pl. 10, figs 4, 8, 9, 11, 15, 17, 18; text-figs 19G, 19K) show a rather similar style of ventral ribbing but are more compressed and the described material is of much larger size, precluding detailed comparison. The closely related genus *Benueites* Reyment, 1954 generally shows a less regular ornament than *Watinoceras*. The inner whorls of one species, *B. trinidadensis* Renz, however, may exhibit a similar style of ribbing and tuberculation to the present material (see Renz 1982: pl. 28, figs 14a, 14b) but they are again much more compressed. The Nigerian specimens may well represent a new species but without knowledge of their outer whorls this matter cannot be decided and it would be premature to describe them as such. Their initial whorls are similar to those in the contemporaneous material referred above to *Watinoceras* aff. *amudariense*. The latter, however, retains its fine ribbing and compressed whorls later into ontogeny. Reyment (1971), impressed by the fact that *Benueites* is frequently to be found represented by finely and coarsely ornamented forms lying side by side, considered that a novel form of ornamental dimorphism characterized the genus. Cooper (1978) doubted this view, as did Renz (1982: 91) who noted that the more coarsely ribbed members in Venezuela occupy a lower stratigraphical position. Cooper (1978: 120–122) himself proposed that *Watinoceras amudariense* was the microconch of *W. coloradoense* (Henderson), a large, coarsely decorated form (see, for example, Cobban & Scott 1972: 76; pl. 27, figs 11–19; pl. 28, figs 1–3, 5–9; text-figs 35–37; Wright & Kennedy 1981: 53, text-figs 18C–F). This suggestion was in turn doubted by Renz (1982: 93), and by Wright & Kennedy (1981: text-fig. 18G) who figured a large, densely ribbed *Watinoceras* which they suggested might represent the macroconch of *W. amudariense*. The nature of any dimorphism shown in *Watinoceras* therefore remains uncertain. It is of interest, however, to note the likeness of the earliest whorls in the two Nigerian forms described here, but whether this similarity has any special significance is difficult to ascertain, especially without the knowledge of their adult whorls.

Genus *MAMMITES* Laube & Bruder, 1887

TYPE SPECIES. *Ammonites nodosoides* Schlüter, 1871; by monotypy.

Mammites nodosoides (Schlüter, 1871)
Figs 18–20, 22

1829 *Ammonites nodosoides* Schlotheim [MS]; von Buch: 424 (nom. nud.).
1871 *Ammonites nodosoides* Schlüter: 19; pl. 8, figs 1–4.
1887 *Mammites nodosoides* Schlotheim sp. Laube & Bruder: 229; pl. 25, figs 1a, 1b.
1903 *Schlutericeras nodosoides* (Schlüter) Hyatt: 111.
1907 *Mammites nodosoides* (Schlotheim); Pervinquière: 309; pl. 18, figs 1a, 1b.
1907 *Mammites nodosoides* var. *afra* Pervinquière: 310; pl. 18, figs 2, 3; text-fig. 18.
1972 *Mammites nodosoides* (Schlotheim); Cobban & Scott: 78 (with synonymy).
1981 *Mammites nodosoides* (Schlüter); Wright & Kennedy: 75; pl. 17, fig. 3; pl. 19, fig. 3; pl. 20, fig. 4; pl. 22, fig. 4; pl. 23, figs 1–3; pl. 24, figs 2, 3; text-figs 19B, 23, 24 (with synonymy).
1982 *Mammites nodosoides* (Schlotheim); Renz: 89; pl. 27, figs 1–10.

MATERIAL AND OCCURRENCE. Seventy-two specimens (C.83517, C.85293–8, C.90327–41, UIN 486.1–50) from the Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria.

REMARKS. This important species occurs abundantly in the upper part of the Lower Turonian at Lokpanta. Variation in the material is slight. The development of the outer ventrolateral tubercles is a little inconsistent. In the later stages they become highly clavate and sometimes fuse with the inner ventrolateral tubercles. Whorl height is greater than whorl breadth in the early and middle stages, but in the largest specimens collected the whorls become rather less compressed and here may resemble those in *Mammites wingi* Morrow (see Cobban & Scott 1972: 79; pl. 26, figs 1–4, 9, 10; pls 31–33; text-fig. 38; Wright & Kennedy 1981: 79; pl. 25, fig. 2; pl. 26, fig. 1; text-figs 25, 27). The inner whorls of *M. wingi* differ, however, in their more delicate ornament while rib density is greater in the adult stages.

Mammites? sp.
Fig. 21a, b

MATERIAL AND OCCURRENCE. A single specimen (C.90360) from the Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria.

REMARKS. This small fragment, probably referable to the genus *Mammites*, shows a rather depressed whorl section. There are broad, rounded ribs, convex on the flanks and bent forwards over the venter, carrying strong umbilical and pointed inner and outer ventrolateral tubercles. Intercalated ribs, bearing outer ventrolateral tubercles alone, are present upon the venter.

Such meagre material is impossible to identify to species level, and even the generic assignment is questionable. It does, however, resemble the inner whorls of the basal Turonian *Mammites dixeyi* Reyment (1955: 50; pl. 9, fig. 4; pl. 10, fig. 3; pl. 11, figs 2a, 2b; text-figs 20, 21) from Nigeria. A *Mammites* from Trinidad (Reyment 1972: 365; fig. 8, 4a, 4b), probably of a somewhat younger age, is also similar, as is *M. nodosoidesappelatus* Etayo-Serna (1979: 85; pl. 13, fig. 1) from Colombia.

Family **VASCOCERATIDAE** Douvillé, 1912
(*nom. correct. & transl.* Spath, 1925; *ex* Vascoceratinés)

Subfamily **VASCOCERATINAE** Douvillé, 1912

Genus ***FAGESIA*** Pervinquière, 1907

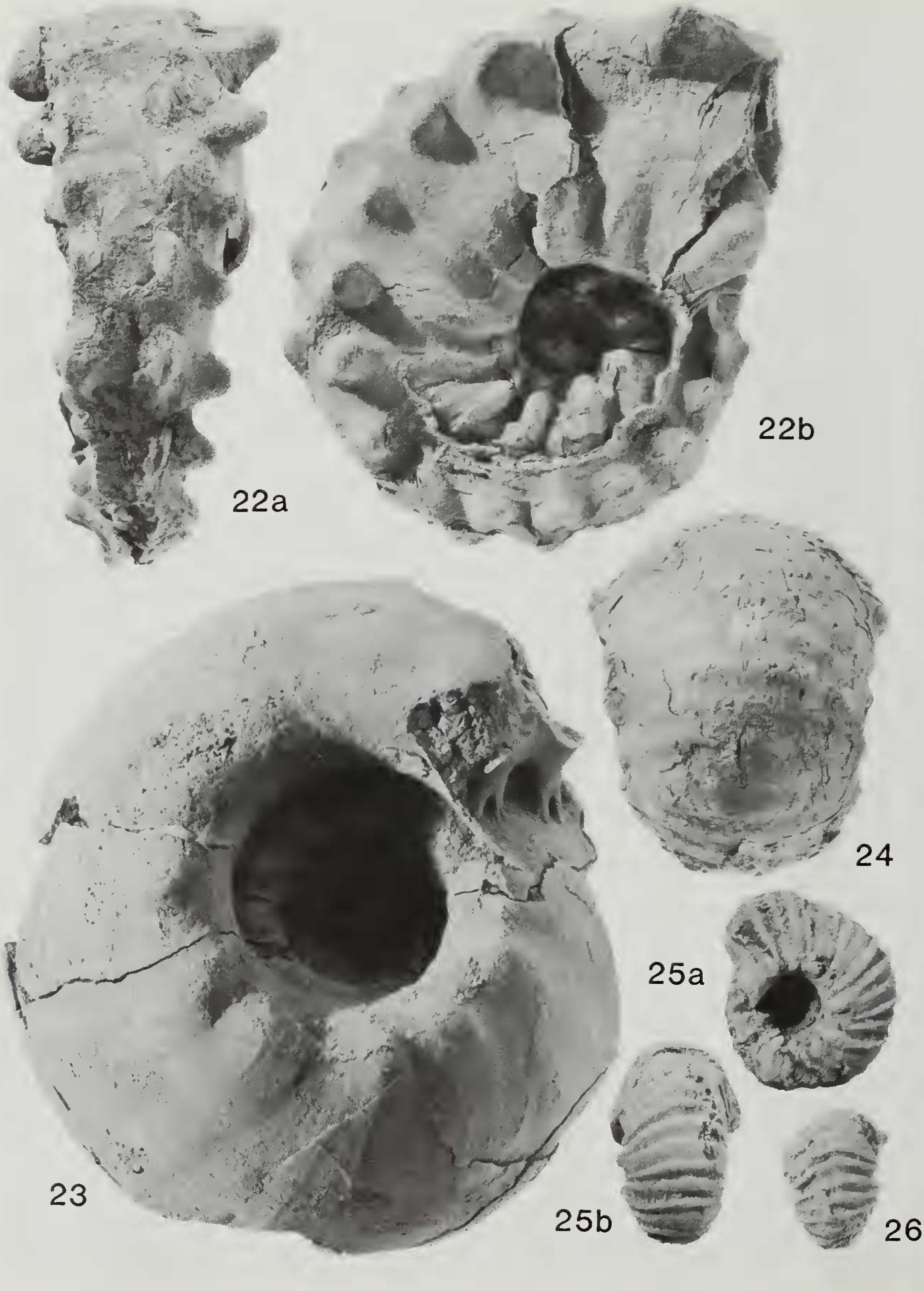
TYPE SPECIES. *Olcostephanus superstes* Kossmat, 1897; by original designation.

Fagesia levis Renz, 1982
Figs 23–4, 27–8

1982 *Fagesia levis* Renz: 78; pl. 22, figs 20a, 20b; pl. 23, figs 1–3; text-figs 53, 59a–c.

MATERIAL AND OCCURRENCE. Twenty-nine specimens (C.85281–3, C.90319–20, UIN 487.1–24) from the Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. A further six specimens (C.90321–6) from the same horizon and locality probably also belong here (Figs 25–6).

DESCRIPTION. Six small specimens (C.90321–6) show what are probably the juvenile whorls of this species. The shell at this stage is evolute and the whorls only slightly depressed with a rounded venter. There are strong, rounded ribs mostly springing in pairs from rather spinose umbilical turbercles and bending forwards over the venter. Intercalated ribs also occur. The ribs fade early in ontogeny and between diameters of about 45 and 60 mm they practically disappear, being represented thereafter by faint, broad folds, convex over the venter. The shell now becomes globular and evolute with 10–11 strong, rounded tubercles at the umbilical shoulder in each whorl. At diameters around 100 mm these tubercles become broader, flatter and less distinct and finally fade out altogether. The maximum diameter attained is about 200 mm. The suture is typical of the genus with highly elongated, much incised elements.


22a
22b
23
24
25a
25b
26

REMARKS. The inner whorls in *Fagesia* characteristically show strong ribs arising in twos or threes from umbilical tubercles. The ornament is generally lost later in ontogeny, the stage at which this occurs being a major factor in distinguishing between species. *F. superstes* (Kossmat 1897: 26; pl. 6, fig. 1; Pervinquière 1907: 322; pl. 20, figs 1–4) shows persistently strong ribbing and umbilical tuberculation, while *F. thevestensis* (Peron 1896: 23; pl. 7, figs 2, 3; Pervinquière 1907: 325; pl. 20, figs 5, 6) and the similar *F. boucheroni* (Coquand) (see Kennedy & Wright 1979*a*: 669, text-figs 1A, 1B) lose their ribbing a little earlier. *F. peroni* Pervinquière (1907: 329; pl. 20, figs 7, 8), on the other hand, loses first its ribbing, then its tuberculation, at a very early ontogenetic stage. The present material is intermediate between *F. peroni* and *F. thevestensis* in these respects. It conforms closely with the globular, evolute, early Turonian *F. levis* Renz (1982: 78; pl. 22, fig. 20; pl. 23, figs 1–3; text-figs 53, 59a–c) from Venezuela. Ontogenetic development in this species is very similar to that in the Nigerian specimens, though juvenile *F. levis* (see Renz 1982: pl. 23, figs 3a, 3b) are rather less densely ribbed than the presumed early whorls in the present Nigerian material (Figs 25–6). At this growth stage the latter is closer to the Colombian *F. zanelli* Etayo-Serna (1979: 89; pl. 13, fig. 11; pl. 14, fig. 5). In this form, however, the ribbing is said to strengthen during ontogeny with prominent narrow ribs persisting up to diameters of at least 50 mm (see Etayo-Serna 1979: pl. 14, fig. 5). Venezuelan specimens occurring with *F. levis* and referred to *F.* aff. *superstes* by Renz (1982: 78; pl. 22, figs 19a, 19b; pl. 23, figs 4a, 4b) differ only in having slightly stronger, more persistent ribbing. The Nigerian material includes forms such as these (Fig. 24); they are probably variants of *F. levis*.

F. bomba (Eck 1909: 179; pl. 17, figs 1, 2), the similar *F. involuta* Barber (1957: 27; pl. 9, fig. 3; pl. 29, figs 6, 7) and *F. simplex* Barber (1957: 27; pl. 8, fig. 1; pl. 29, figs 4, 5) all lose their ribbing early, but the first two species are markedly more involute than the present material, while *F. simplex* has a much simpler suture pattern. *F. lenticularis* Freund & Raab (1969: 36–42; pl. 6, figs 3–7; pl. 7, figs 1–3; pl. 8, figs 1, 2; text-figs 7h–k, 8a–i, 9a–c) and its varieties have a peculiar, eccentric mode of coiling. *F. rudra* (Stoliczka 1865: 122; pl. 60, fig. 1; Kennedy & Wright 1979*a*: 666; pl. 82, figs 1, 2) lacks umbilical tubercles. *F. pachydiscoides* Spath (see Wright & Kennedy 1981: 97, text-fig. 37) is more compressed. In addition, its umbilical tubercles persist to a very late stage, as is the case in *F. catinus* (Mantell) (see Wright & Kennedy, 1981: 88; pl. 26, fig. 2; text-figs 31–36, for review and synonymy) where they increase in strength during ontogeny. The ribbing also persists longer in *F. catinus* (see Powell 1963: 320; pl. 33, fig. 2; pl. 34, figs 1–5).

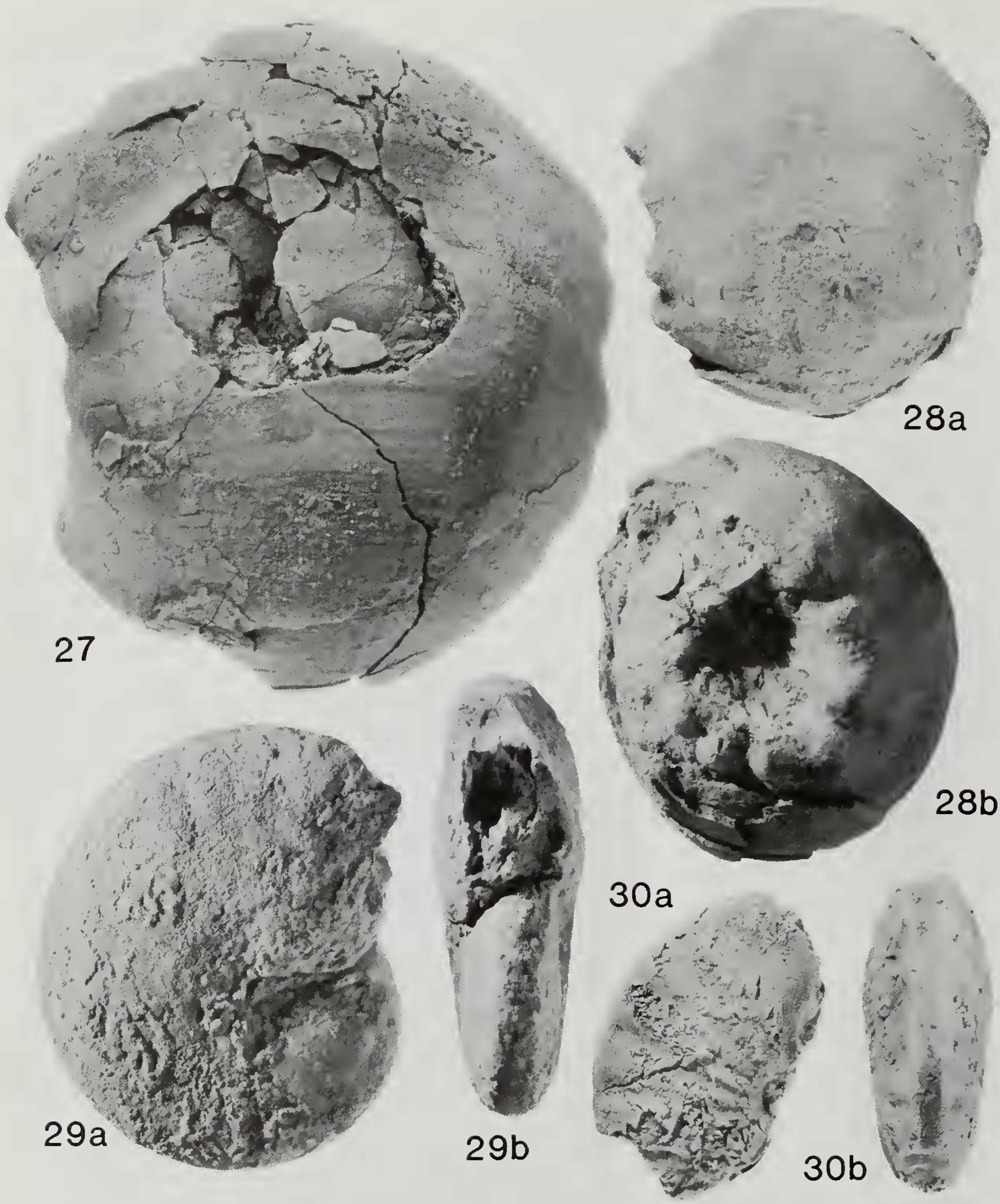
Genus *NEOPTYCHITES* Kossmat, 1895

TYPE SPECIES. *Ammonites telinga* Stoliczka, 1865 (= *A. cephalotus* Courtiller, 1860); by original designation.

Neoptychites cephalotus (Courtiller, 1860)
Figs 31–2

1860 *Ammonites cephalotus* Courtiller: 248; pl. 2, figs 1–4.
1865 *Ammonites xetra* Stoliczka: 124; pl. 61, figs 1, 2.
1865 *Ammonites telinga* Stoliczka: 125; pl. 62, figs 1, 2.
1895 *Neoptychites xetra* (Stoliczka) Kossmat: 72.
1895 *Neoptychites telinga* (Stoliczka) Kossmat: 71; pl. 7, fig. 1.

Fig. 22a, b *Mammites nodosoides* (Schlüter). Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. C.90327, × 1. See also Figs 18–20.
Figs 23–24 *Fagesia levis* Renz. Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Fig. 23, C.90319, × 1. Lateral view of specimen shown in Fig. 27. Fig. 24, C.90320, × 1. A variant with abnormally persistent ribbing. See also Figs 25–26(?), 27–28.
Figs 25–26 *Fagesia levis* Renz?. Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. The presumed early whorls. Fig. 25a, b, C.90321, × 1. Fig. 26, C.90322, × 1.



Figs 27–28 *Fagesia levis* Renz. Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Fig. 27, C.90319, × 1. Ventral view of specimen shown in Fig. 23. Fig. 28a, b, C.85282, × 1. See also Figs 23–24, 25–26(?).

Fig. 29a, b *Thomasites gongilensis* (Woods). Eze-Aku Formation (uppermost Cenomanian or lowermost Turonian), Ezillo, south-east Nigeria. C.90354, × 1. See also Figs 34–35.

Fig. 30a, b *Herrickiceras*? sp. Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. C.85287, × 1.

1907 *Neoptychites cephalotus* (Courtiller) Pervinquière: 393; pl. 27, figs 1–4; text-fig. 152.
1907 *Neoptychites gourguechoni* Pervinquière: 400; pl. 27, figs 8, 9; text-figs 155, 156.
1979*a* *Neoptychites cephalotus* (Courtiller); Kennedy & Wright: 670; pl. 82, figs 3–5; pl. 83, figs 1–3; pl. 84, fig. 3; pl. 85, figs 1–5; pl. 86, figs 5, 6; text-fig. 2 (with synonymy).
?1979 *Franciscoites suarezi* Etayo-Serna: 87; pl. 13, fig. 2; text-figs 8X, Y, ü.
1982 *Neoptychites* aff. *crassus* Solger; Renz: 88; pl. 26, figs 16a, 16b.
1982 *Neoptychites* aff. *telingaeformis discrepans* Solger; Renz: 88; pl. 26, figs 17a, 17b.
?1982 *Neoptychites transitorius* Renz: 87; pl. 26, figs 15, 18; text-figs 65d, 66A, 66a–d.

MATERIAL AND OCCURRENCE. At least five specimens, four (C.83512, C.85289, C.90317–8) from the Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria; the other (C.90359) from a slightly lower (basal Turonian) horizon at Lokpanta.

REMARKS. This material is identical with *Neoptychites cephalotus* (Courtiller). The smallest specimen (C.90359), with a diameter of 21 mm, is moderately compressed, shows a sharply rounded venter and has the characteristic collared constrictions of the juveniles in this species (see, for example, Solger 1904: pl. 3, fig. 4; Pervinquière 1907: pl. 37, figs 3a, 3b; Riedel 1932: pl. 26, fig. 5; Reyment 1972: fig. 7, 1–3; Renz 1982: pl. 26, figs 17a, 17b; Cobban & Hook 1983: pl. 3, figs 9–11). *Franciscoites suarezi* Etayo-Serna (1979: 87; pl. 13, fig. 2), known only from juveniles, is also very similar and seems to be a synonym. The largest Nigerian specimen (C.85289) has a diameter of some 200 mm. It is adult and shows the distinctive constricted aperture of this species. Its whorls are smooth and triangular, the venter being narrowly rounded and raised up slightly along the median line on the early part of the body chamber.

Kennedy & Wright (1979*a*: 670–680) have discussed the genus *Neoptychites* at length. They treated *N. xetriformis* Pervinquière as a distinct species but noted its association with *N. cephalotus* in the Touraine area of France and raised the possibility of the two being dimorphs. Cobban & Hook (1983: 14–15), working with large collections from New Mexico, considered *N. xetriformis* to be a synonym of *N. cephalotus*. They regarded the latter species as highly variable, including both small, stout, ribbed forms of *N. xetriformis* character, as well as larger, slender, more weakly ornamented individuals having the form of *N. cephalotus*. They, too, suggested dimorphism but were disturbed by the lack of a clearly bimodal size pattern within the population. The Nigerian material is too sparse to contribute greatly to this problem and a conservative approach is followed here. It may be relevant, however, that along with the material from the *Mammites nodosoides* Zone at Lokpanta there comes a rather poorly preserved specimen (C.85288) of 90 mm diameter which shows broad whorls, a rounded venter and distinct, broad ribs. This individual is close to *N. xetriformis*, adding to the evidence for its coexistence with *N. cephalotus*.

Kennedy & Wright (1979*a*: 680–681) showed that in France *Neoptychites* occurs some way up in the Turonian, above beds with *Mammites* of the *nodosoides* group. They regarded it as being approximately contemporaneous elsewhere in the world except for the western interior of the United States (Colorado) where it appears in the basal Turonian Zone of *Watinoceras coloradoense* (see Cobban & Scott 1972; Kauffman *et al.* 1978). The Nigerian material confirms this early occurrence of the genus, it being found below beds with *Mammites nodosoides*.

Subfamily **PSEUDOTISSOTIINAE** Hyatt, 1903

Genus ***THOMASITES*** Pervinquière, 1907

TYPE SPECIES. *Pachydiscus rollandi* Peron, 1889; by original designation.

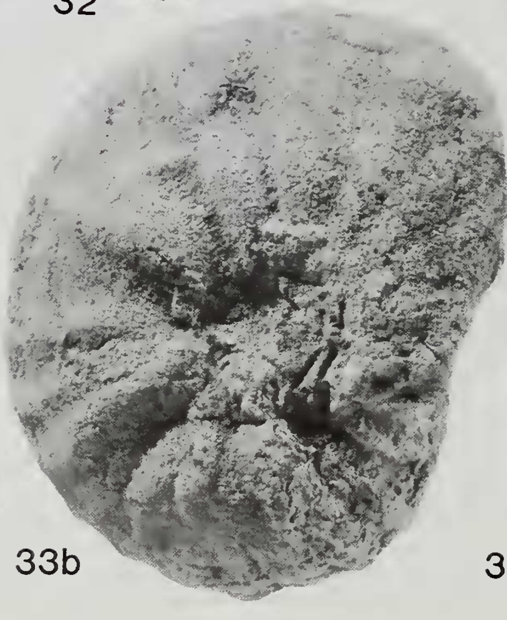
REMARKS. The close similarity between *Thomasites* and *Gombeoceras* Reyment has been remarked upon by several authors. Basse (1940: 457) included *Vascoceras gongilense* Woods, the type species of *Gombeoceras*, under synonymy in *Thomasites*. Reyment (1954: 151), in proposing the genus *Gombeoceras*, differentiated it from *Thomasites* by its more evolute shell, less triangular whorls, weaker umbilical tuberculation and non-constricted aperture. Freund & Raab (1969: 42–43), however, considered the morphological range in *Thomasites* to be wide enough to include *Gombeoceras*. They noted that the Nigerian material of *Gombeoceras* figured


31a


32


31b


33a


33b


33c

by Reyment (1954, 1954*a*, 1955) and Barber (1957) consisted entirely of phragmocones, the nature of the adult aperture being unknown. In fact, an undescribed, entire, adult specimen of *G. gongilense* (C.47561) from the Numan area of north-east Nigeria does indeed show the moderately constricted aperture characteristic of adult *Thomasites rollandi* (see Pervinquière 1907: pl. 22, figs 4a, 4b). The Nigerian specimen has a diameter of 130 mm; in *T. rollandi* the constricted aperture appears at diameters of 110–130 mm (Pervinquière 1907: 343). Reyment (1979) sought to maintain the separate status of *Gombeoceras*, stressing that *Thomasites* lacks a median or ventrolateral keel at any ontogenetic stage. Wright & Kennedy (1981: 99), however, pointed out that the siphonal ornament is highly variable in both *Thomasites* and *Gombeoceras*, and they could find no character to distinguish between the two. In view of their clear similarity, this latter view is followed here, *Gombeoceras* being treated as a synonym of *Thomasites*.

Thomasites gongilensis (Woods, 1911)
Figs 29, 34–5

1911 *Vascoceras gongilense* Woods: 282; pl. 21, fig. 7; pl. 22, fig. 1.
1954 *Gombeoceras gongilense* (Woods) Reyment: 151; pl. 2, fig. 1; pl. 3, fig. 6; text-fig. 1.
1954*a* *Gombeoceras subtenue* Reyment: 261; pl. 4, fig. 4; text-fig. 3f.
1955 *Gombeoceras gongilense* (Woods); Reyment: 63; pl. 14, fig. 5; pl. 21, fig. 4.
1957 *Gombeoceras gongilense* (Woods); Barber: 79; pl. 17, figs 1–6; pl. 18, figs 1–4; pl. 19, figs 1–6; pl. 20, fig. 3; pl. 37, figs 1–20.
1965 *Gombeoceras gongilense* (Woods); Reyment: pl. 2, fig. 3; pl. 3, figs 16, 19.
1976 *Gombeoceras gongilensis* (Woods); Offodile: 69; pl. 12, fig. 3.
1976 *Gombeoceras compressum* Barber; Offodile: 69; pl. 12, fig. 4.
1976 *Gombeoceras gongilense* (Woods); Offodile & Reyment: 58, text-figs 31, 32.
1976 *Gombeoceras compressum* Barber; Offodile & Reyment: 59, text-fig. 33.
1981 *Thomasites gongilensis* (Woods) Wright & Kennedy: 100; pl. 24, fig. 1; pl. 25, fig. 1.

MATERIAL AND OCCURRENCE. Two specimens (C.90353–4) from the Eze-Aku Formation (uppermost Cenomanian or lowermost Turonian), Ezillo, south-east Nigeria. A further specimen (C.90355) from the same horizon and locality may also belong here.

REMARKS. Barber (1957) demonstrated very clearly the wide degree of variation shown by populations of *Thomasites gongilensis* in north-east Nigeria. He suspected, but was unable to prove, that this variability was partly stratigraphical and geographical as well as individual in nature. He therefore separated his diverse morphotypes into a number of subspecies. Reyment (*in* Offodile & Reyment 1976: 53), however, preferred to regard these forms as separate species. In as much as they occur side by side or within a few metres of section in both the middle Benue Valley and north-eastern regions of Nigeria (Barber 1957, Offodile & Reyment 1976, Wozny & Kogbe 1983) and that they tend to grade into one another, it is probably more correct to regard them as mere varieties of *T. gongilensis*. Wright & Kennedy (1981: 100) suspected that a similar situation might prove to exist amongst the Tunisian populations of *Thomasites* described by Pervinquière (1907); all these forms may be varieties of *T. rollandi* (Peron).

Two varieties of *T. gongilensis* have been identified from Ezillo. The first (C.90354, Fig. 29a, b) is compressed, involute and with flattened flanks and a rounded venter. There are feeble ribs on the outer parts of the flank and venter; the latter also bears weak ventrolateral and siphonal tubercles. In all these respects, as in suture pattern, this specimen conforms closely with the variety *T. gongilensis* var. *compressus* (see Barber 1957: 41; pl. 19, figs 2a, 2b, 5a, 5b; pl. 33, figs 15, 16), the most compressed and one of the most feebly ornamented varieties of this species. The Tunisian form named *T. meslei* by Pervinquière (1907: 345; pl. 22, figs 8, 9) is very

Figs 31–32 *Neoptychites cephalotus* (Courtiller). Fig. 31a, b, C.85289, ×0·65. Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Fig. 32, C.90359, × 1. Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria; latex cast.

Fig. 33a–c *Thomasites koulabicus* (Kler). Eze-Aku Formation (uppermost Cenomanian or lowermost Turonian), Ezillo, south-east Nigeria. C.90352, × 1.

close to *T. gongilensis* var. *compressus*. Wright & Kennedy (1981: 100) noted the morphological overlap between the Tunisian and Nigerian populations of *Thomasites* but because the former was poorly preserved were unable to decide whether *T. gongilensis* should be brought into synonymy under *T. rollandi*.

The second specimen (C.90353, Fig. 34a, b) is moderately evolute and moderately compressed, though slightly crushed laterally. Its venter is broadly rounded at first but shows a low siphonal ridge later in ontogeny. There are low, rounded ribs upon the inner two-thirds of the flanks. The ventral ornament is weak at first but at its adoral end the specimen shows strong ventrolateral tubercles and clavate swellings upon the siphonal ridge. Two varieties of *T. gongilensis* resemble this specimen in their later whorls. *T. gongilensis* var. *inflatus* (Barber 1957: 43; pl. 18, figs 3, 4; pl. 33, figs 18–20) shows weakened ornament and a broad keel in its later stages but is more inflated. Rather closer is *T. gongilensis* var. *tectiformis* (Barber 1957: 41; pl. 17, figs 1–4; pl. 19, fig. 6; pl. 33, figs 4–6; Fig. 35) which, while displaying angular ventrolateral shoulders in its early whorls, develops a more rounded whorl section towards adulthood, when its ornament weakens though the keel persists.

A third Ezillo specimen (C.90355) has the overall dimensions of *T. gongilensis* var. *costatus* (Barber 1957: 41; pl. 18, fig. 1; pl. 19, figs 1, 3; pl. 37, figs 9, 10) but is too poorly preserved for certain identification.

In Nigeria, *Thomasites* has previously been reported from only one locality south of the Benue River, a section in the Konshisha River near Oturkpo (Reyment 1955: 63, 98; Fig. 46, p. 58). The present records, therefore, considerably extend its southerly geographical range.

Thomasites koulabicus (Kler, 1909)
Fig. 33a–c

1909 *Pseudotissotia koulabica* Kler: 157; pl. 6, figs 1–3; pl. 7, figs 1, 2; pl. 8, figs 1, 2.
1954*a* *Gombeoceras koulabicum* (Kler) Reyment: 261.
1958 *Thomasites koulabicus* (Kler) Tsagareli, Glazunova, Luppov & Mikhailov (*in* Orlov): 124; pl. 61, figs 3a, 3b; text-fig. 99b.
1966 *Koulabiceras koulabicum* (Kler) Atabekyan: 77.
1969 *Gombeoceras* (*Ferganites*) *koulabicum* (Kler); Stankievich & Pojarkova: 94; pl. 2, figs 3a, 3b; pl. 3, figs 1a, 1b.
?1969 *Gombeoceras* (*Ferganites*) *kanicum* Stankievich & Pojarkova: 95; pl. 3, figs 2a, 2b.
1969 *Gombeoceras* (*Ferganites*) *kleri* (Luppov MS) Stankievich & Pojarkova: 96; pl. 4, figs 1–3.
1981 *Thomasites koulabicus* (Kler); Wright & Kennedy: 100.

Material and occurrence. A single specimen (C.90352) from the Eze-Aku Formation (uppermost Cenomanian or lowermost Turonian), Ezillo, south-east Nigeria.

Description. This specimen is moderately evolute. At first its whorls are rather inflated and the venter arched, but the body chamber becomes compressed with flatter flanks and a broadly rounded venter. The ornament of the phragmocone is very coarse; massive umbilical bullae give off pairs of strong, rounded ribs, while additional intercalated ribs arise some distance down the flanks. There are prominent ventrolateral tubercles, and clavate siphonal tubercles which tend to fuse so producing an intermittent keel. Upon the body chamber the ornament weakens, the ribs becoming flatter and lower, though the umbilical tubercles remain prominent.

Remarks. As Tsargareli *et al.* (*in* Orlov 1958: 124) and Wright & Kennedy (1981: 99) have pointed out, *Pseudotissotia koulabica* Kler (1909: 157; pls 6–8), previously unknown outside Soviet Central Asia, is a *Thomasites*. It represents the most coarsely ornamented member of the genus yet known. Reyment (1954*a*: 261) and Barber (1957: 39, 45) were of the opinion that the morphological range of *T. gongilensis* overlaps that of *T. koulabicus*. Wright & Kennedy (1981: 99–100) preferred to maintain the two as distinct species. Since the ornament in *T. koulabicus* is consistently stronger than that in even the most coarsely decorated variety of *T. gongilensis*, *T. gongilensis* var. *crassicostatus* (Barber 1957: 45; pl. 18, figs 2a, 2b; pl. 33, figs 7, 8), and since the adult body chamber appears to undergo wholesale compression at adulthood (see Figs 33a, c; Kler 1909: pl. 8, fig. 1; Stankievich & Pojarkova 1969: pl. 3, figs 1a, 1b) rather than merely showing a constricted aperture like that in *T. gongilensis*, Wright & Kennedy's view is followed here. The size at which compression of the body chamber takes place in *T. koulabicus* is, however, variable. In the present material it takes place at an overall diameter of some 85 mm (phragmocone diameter 55 mm) when the ornament becomes effaced, indicating adulthood. In specimens figured by Kler (1909: pl. 7, figs 1, 2; pl. 8, fig. 1) these characters do not appear until phragmocone diameters of 90–95 mm and certain specimens (see Kler 1909: 157–158) reach overall diameters of nearly 150 mm. Perhaps this size difference reflects dimorphism.

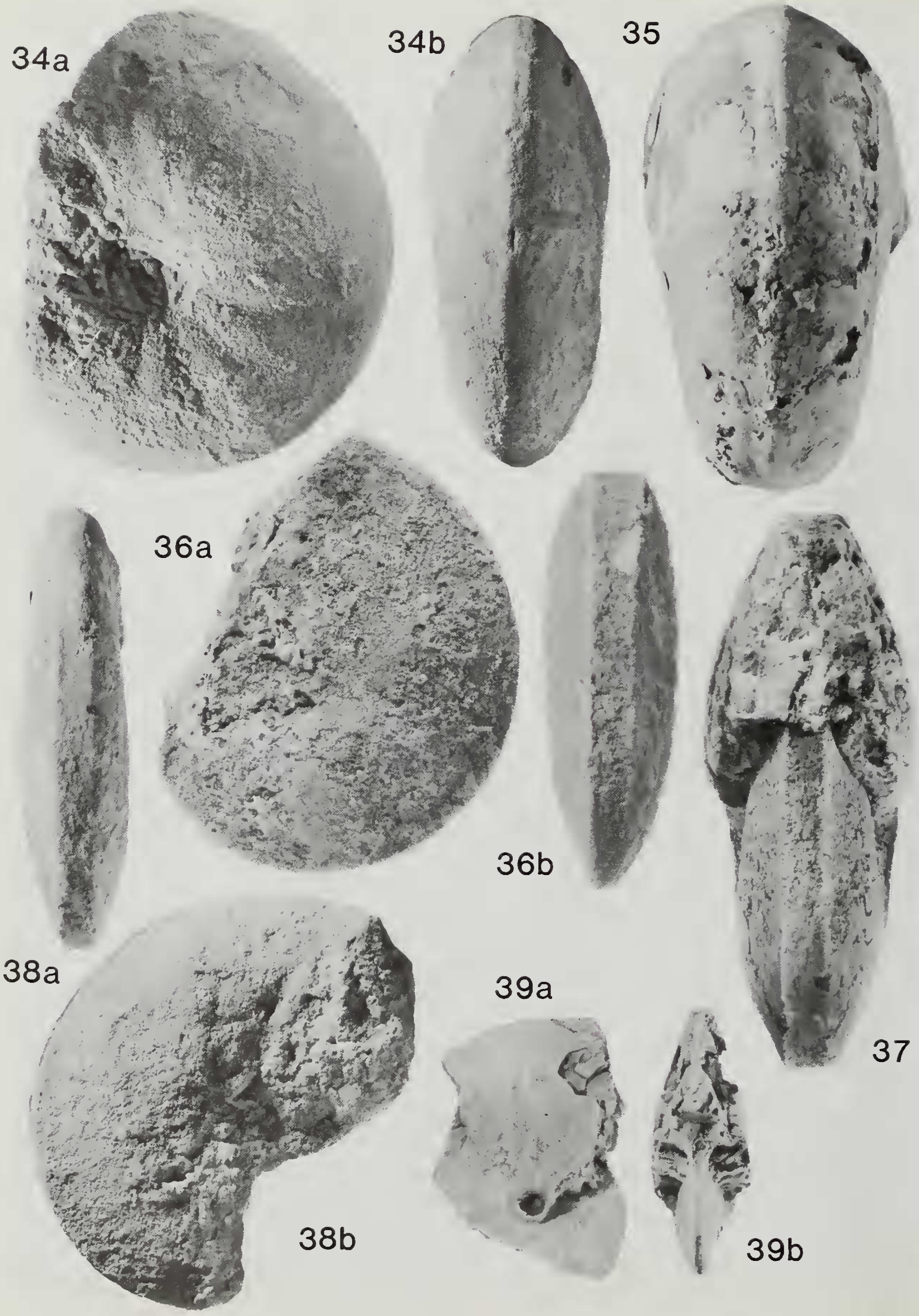
The genus *Koulabiceras* Atabekyan, 1966 (type species *Pseudotissotia koulabica* Kler) is a subjective synonym of *Thomasites*. *Gombeoceras* (*Ferganites*) Stankievich & Pojarkova (1969: 94) shares this type species and is therefore an objective synonym of *Koulabiceras*. Stankievich & Pojarkova (1969) referred the following species to *G.* (*Ferganites*): *G.* (*F.*) *koulabicum* (Kler), *G.* (*F.*) *kleri* Stankievich & Pojarkova (1969: 96; pl. 4, figs 1–3) and *G.* (*F.*) *kanicum* Stankievich & Pojarkova (1969: 95; pl. 3, figs 2a, 2b). The last of these has rather broad whorls, especially in its later growth stages. All three are nevertheless similar and, bearing in mind the wide degree of variation shown by species of *Thomasites*, all three probably belong in *T. koulabicus* (see also Wright & Kennedy 1981: 100). Stankievich & Pojarkova (1969: 91–93; pl. 1, figs 2, 3; pl. 2, figs 1, 2) described several additional *Thomasites* from the Soviet Union as *T.* cf. *globosotuberculatus* Pervinquière, *T.* cf. *jordani* Pervinquière and *T.*(?) *inflatus* sp. nov. These show a consistently strong ornament which is only rarely approached by the Tunisian material described by Pervinquière (1907). All the central Asiatic forms come from a similar stratigraphical horizon (Stankievich & Pojarkova 1969: 87–88) and one might speculate that, just as in the cases of the Tunisian and north-east Nigerian populations of *Thomasites*, they represent a complex of variants all belonging to the single coarsely ornamented species *T. koulabicus*.

Genus ***WRIGHTOCERAS*** Reyment, 1954

TYPE SPECIES. *Bauchioceras* (*Wrightoceras*) *wallsi* Reyment, 1954; by original designation.

REMARKS. Members of this genus were first described from the Lower Turonian of Tunisia as *Hoplitoides munieri* Pervinquière (1907: 217; pl. 10, figs 1, 2) and *H. mirabilis* Pervinquière (1907: 218; pl. 10, fig. 3). Pervinquière (1907: 215–216) was aware that these forms were untypical of *Hoplitoides* von Koenen in that they exhibit tabulate venters not in the juvenile stages alone but throughout ontogeny. Rather than refer them to a new genus, however, he preferred to emend the diagnosis of *Hoplitoides* (see Solger 1904) and recognized within it two groups, those with tabulate venters throughout growth and those with narrowly rounded or sharpened venters in their later stages. He regarded the former group as ancestral to the latter. Kummel & Decker (1954) described similar, broad-ventered material from northern Mexico as '*Hoplitoides*' cf. '*H.*' *munieri* Pervinquière but indicated that it did not truly belong in this genus and should be included in a new taxon (see also Benavides-Cáceres 1956: 476). Reyment (1954), working primarily with material from northern Nigeria, proposed *Wrightoceras*, originally as a subgenus of *Bauchioceras* Reyment, 1954, in which he included *B.* (*W.*) *wallsi* as type species along with *Hoplitoides munieri* and *H. mirabilis*. Later, Reyment (1955) treated both *Bauchioceras* and *Wrightoceras* as subgenera of *Pseudotissotia* Peron, *Wrightoceras* being distinguished mainly by its lack of a siphonal keel. Barber (1957) followed this procedure. Kennedy, Cooper & Wright (1979) re-examined *Ammonites gallienni* d'Orbigny, the type species of *Pseudotissotia*, and suggested that *Bauchioceras* be treated as a strict synonym of *Pseudotissotia*. *Wrightoceras*, however, was maintained as a separate genus altogether since it shows at most a feeble siphonal keel in the juvenile stages only and possesses comparatively weak, impersistent ornament.

At present, the following can be referred to *Wrightoceras*: *W. wallsi* Reyment, *W. munieri* (Pervinquière), of which *W. mirabilis* (Pervinquière) may be a synonym, *W. inca* (Benavides-Cáceres), *W. llarenai* (Karrenberg), *W. submunieri* Wiedmann and *W. reymenti* Collignon & Roman. *Pseudotissotia gagnieri* Faraud (1951: 149; pl. 5, fig. 1) may also belong here but develops an untypical rounded venter. The Colombian genus *Imlayiceras* Leanza, 1967 (type species *Imlayiceras washbournei* Leanza 1967: 198; pl. 4, figs 1–4; pl. 6, figs 1, 4–6) differs from *Wrightoceras* only in the reported presence of faint constrictions on the early whorls. The later


34a
34b
35
36a
36b
37
38a
38b
39a
39b

stages in the two genera are, however, indistinguishable and the Colombian material is perhaps better included in *Wrightoceras* also.

The relative stratigraphical positions of *Wrightoceras* and *Hoplitoides* are discussed below (p. 53).

Wrightoceras wallsi Rement, 1954
Figs 36–7

1954 *Bauchioceras* (*Wrightoceras*) *wallsi* Reyment: 160; pl. 2, fig. 4; pl. 3, figs 3, 3a.
1955 *Pseudotissotia* (*Wrightoceras*) *wallsi* (Reyment) Reyment: 71; pl. 24, fig. 1; text-figs 32a, 32c, 32d.
1957 *Pseudotissotia* (*Wrightoceras*) *wallsi* (Reyment); Barber: 53; pl. 24, figs 1, 2; pl. 34, figs 5, 13.
1965 *Pseudotissotia* (*Wrightoceras*) *wallsi* (Reyment); Reyment: pl. 4, figs 14–17.

MATERIAL AND OCCURRENCE. Two specimens (C.90349–50) from the Eze-Aku Formation (Lower Turonian), Ezillo, south-east Nigeria.

REMARKS. Barber (1957: 51) found populations of *Wrightoceras wallsi* to show a variable degree of compression. The two present specimens represent relatively slim variants and tend towards the material referred below to *W.* cf. *munieri* (Pervinquière). The smaller of the two (C.90349, Fig. 36a, b), with a diameter of 70 mm, has at first a slightly concave venter bordered by ventrolateral keels, becoming more tabulate later. It is exactly comparable with an individual of *W. wallsi* (C.47617, Fig. 37) from Kanawa near Gombe in north-east Nigeria at an equivalent size. The larger of the two specimens (C.90350) has a diameter of 240 mm and, apart from having a slightly more rounded adult venter, is very close to the large form from Deba-Habe near Gombe (C.47421) figured by Reyment (1955: pl. 24, fig. 1).

Material from northern Mexico described by Kummel & Decker (1954: 317; pl. 33, figs 1, 2; text-figs 7, 10) as '*Hoplitoides*' cf. '*H.*' *munieri* Pervinquière has a rather broader and more sulcate venter than Pervinquière's species, as these authors pointed out. It is close to *W. wallsi* but shows weak ribs on the flanks which sometimes cross the venter.

Wrightoceras cf. **munieri** (Pervinquière, 1907)
Figs 38, 40

cf. 1907 *Hoplitoides munieri* Pervinquière: 217; pl. 10, figs 1, 2.
cf. 1907 *Hoplitoides mirabilis* Pervinquière: 218; pl. 10, fig. 3.
cf. 1969 *Hoplitoides* cf. *H. mirabilis* Pervinquière; Freund & Raab 65; pl. 10, figs 1, 2; text-figs 13i–l.
cf. 1982 *Hoplitoides munieri* Pervinquière; Renz: 100; pl. 31, figs 3, 4, 6, 11.
cf. 1982 *Hoplitoides* cf. *munieri* Pervinquière; Renz: 100; pl. 31, fig. 5.

MATERIAL AND OCCURRENCE. Four specimens (C.90345–8) from the Eze-Aku Formation (Lower Turonian), Ezillo, south-east Nigeria.

DESCRIPTION. These forms are compressed, involute and smooth at all observed growth stages. The early whorls are a little inflated in the mid-flank region and have a moderately broad, sulcate venter up to a diameter of about 60 mm. The flanks later become more flattened and the venter tabulate. At diameters in excess of 70 mm the ventrolateral shoulders become rounded. The suture is not displayed.

Figs 34–35 *Thomasites gongilensis* (Woods). Fig. 34a, b, C.90353, × 1. Eze-Aku Formation (uppermost Cenomanian or lowermost Turonian), Ezillo, south-east Nigeria. Fig. 35, C.47555, × 1. Dukul Formation (uppermost Cenomanian or lowermost Turonian), near Numan, north-east Nigeria. See also Fig. 29a, b.

Figs 36–37 *Wrightoceras wallsi* Reyment. Fig. 36a, b, C.90349, × 1. Eze-Aku Formation (Lower Turonian), Ezillo, south-east Nigeria. Fig. 37, C.47617, × 1. Pindiga Formation (Lower Turonian), Kanawa, north-east Nigeria.

Fig. 38a, b *Wrightoceras* cf. *munieri* (Pervinquière). Eze-Aku Formation (Lower Turonian), Ezillo, south-east Nigeria. C.90347, × 1. See also Fig. 40.

Fig. 39a, b *Hoplitoides latefundatus* sp. nov. Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Paratype C.85284, × 1. See also Figs 41–44.

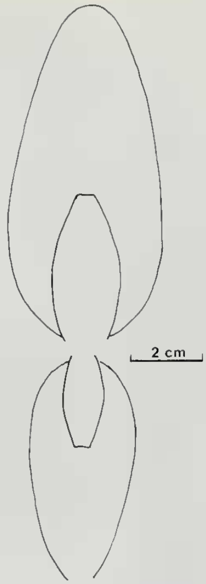


Fig. 40 Whorl section in *Wrightoceras* cf. *munieri* (Pervinquière). Based on specimen C.90345. See also Fig. 38a, b.

REMARKS. These specimens differ from the material referred above to *Wrightoceras wallsi* in their rather narrower venters which tend to become more distinctly rounded on the later whorls. The differences are, however, more of degree than kind and the two forms tend to grade into one another in the Ezillo population. The closest previously described species is *W. munieri* (Pervinquière) which is distinguished from its contemporary *W. mirabilis* (Pervinquière) on sutural grounds alone. These two have virtually identical gross morphologies and, as suggested by Reyment (1954: 157), Benavides-Cáceres (1956: 476) and Barber (1957: 53), they may be synonyms. Comparable material occurs in the Lower Turonian of the Negev, the *Hoplitoides* cf. *mirabilis* of Freund & Raab (1969: 65; pl. 10, figs 1, 2), and in Venezuela, the *H. munieri* and *H.* cf. *munieri* of Renz (1982: 100; pl. 31, figs 3–6, 11). Poorly preserved specimens from northern Mexico described by Böse (1920: 225; pl. 19, figs 1–3) also seem to be closely related.

Wrightoceras inca (Benavides-Cáceres 1956: 475; pl. 63, figs 6–11) is another similar form, said to be distinguished from *W. munieri* by faint, falciform ribs on the inner whorls. *W. submunieri* Wiedmann (see Wiedmann 1975: figs 6A–C; 1979: pl. 8, fig. 1; Wiedmann & Kauffman 1978: pl. 8, fig. 2) has a broader venter, more inflated inner flanks and strong ribbing on the early whorls; it resembles *W. llarenai* (Karrenberg 1935: 143; pl. 31, fig. 14; pl. 33, fig. 14). *W.*(?) *gagnieri* (Faraud 1951: 149; pl. 5, fig. 1) develops a rounded venter with flank ribbing terminating in ventrolateral tubercles. *W. reymenti* Collignon & Roman (*in* Amard *et al.* 1981: 57; pl. 9, figs 7a, 7b) has a very wide umbilicus, highly inflated whorls and a very broad, tabulate venter.

Family **COILOPOCERATIDAE** Hyatt, 1903

Genus ***HOPLITOIDES*** von Koenen, 1898

TYPE SPECIES. *Hoplitoides latesellatus* von Koenen, 1898 (=*Neoptychites ingens* von Koenen, 1897); by original designation.

REMARKS. The genus *Hoplitoides* includes involute, slender ammonites in which the venter is sulcate or flattened in the initial whorls and becomes sharp or narrowly rounded later on. The early whorls may be ribbed, with ventrolateral tubercles and umbilical bullae developed in some species. The suture possesses a very wide lateral lobe. The taxonomic history and occurrence of *Hoplitoides* has been reviewed by Cobban & Hook (1980: 5–6). Pervinquière (1907: 216) suggested that its ancestors were to be found amongst forms now included in

Wrightoceras which retain broad venters until adulthood. Reyment (1954: 157–158) at first doubted this view but subsequently (Reyment 1954*a*: 261; 1955: text-fig. 31) indicated just such a scheme, deriving *Hoplitoides* from *Wrightoceras*. Cobban & Hook (1980: 6) alternatively suggested that the ancestral form may have been *Choffaticeras* Pervinquière. The Nigerian material described here suggests that *Hoplitoides* was indeed derived from *Wrightoceras*, by way of forms such as those referred above to *W.* cf. *munieri*. These show a very broadly rounded venter in their adult stages but the juvenile whorls are close to those in slender *W. wallsi*. Certain forms belonging in this group show a suture pattern intermediate between those characteristic of *Wrightoceras* and *Hoplitoides* (see Pervinquière 1907: text-fig. 84; Freund & Raab 1969: text-figs 13j, 13l). As Pervinquière (1907: 218–219) noted, such types differ from the relatively simple pattern typical of *Wrightoceras* not in their basic construction, but in the accentuation of their subdivisions.

The Nigerian material of *W.* cf. *munieri* seems to be of very early Turonian age (see pp. 58–9). The upper part of the Lower Turonian at Lokpanta yields apparently more advanced transitional forms described below as *Hoplitoides latefundatus* sp. nov. These retain truncated venters until relatively large diameters of 65–75 mm but show a suture pattern like that in other *Hoplitoides* with a deep, wide lateral lobe even at a very early growth stage. The main occurrence of *Hoplitoides* in Nigeria is at Wadatta near Makurdi, where a thin limestone contains *H. ingens* (von Koenen), *H. gibbosulus* (von Koenen), *H.* cf. *wohltmanni* (von Koenen), *H. koeneni* Solger and *H. crassicostatus* Reyment. Reyment (1955) originally assigned this fauna an early Turonian age but later (Reyment 1978: 2) revised this to early Middle Turonian.

In the western interior of the United States *Hoplitoides* occurs only in New Mexico. The earliest recorded forms come from the lower part of the Zone of *Collignoniceras woollgari* (Mantell) of early Middle Turonian age. This material includes specimens comparable to *H. wohltmanni* (see Cobban & Hook 1979: 19; pl. 4, figs 3, 4; text-figs 10, 11; 1980: 7; pl. 1, figs 3, 4; text-figs 4, 5; 1981) but retaining truncated venters to a large diameter, and others close to *H. koeneni* (see Cobban & Hook 1979: 19; pl. 4, figs 1, 2; 1980: 6; pl. 1, figs 1, 2; pl. 3, figs 4, 5), again showing persistent truncation of the venter. *H. sandovalensis* Cobban & Hook (1980: 8; pl. 2; pl. 3, figs 6–8, 12–16; pl. 4; pl. 11, fig. 1; pl. 18, figs 4–6; text-figs 6, 7), a species developing a sharp venter at a very early ontogenetic stage, appears in the overlying Zone of *Prionocyclus hyatti* (Stanton).

Elsewhere in the world, specimens close to *Wrightoceras munieri* (see Freund & Raab 1969: 65; pl. 10, figs 1, 2) occur in 'Zone 6' in Israel, towards the top of these authors' Lower Turonian. In Venezuela similar forms (Renz 1982: pl. 31, figs 3, 5) are amongst the earliest Turonian ammonites known, occurring in Renz' (1982: 72–73) 'Assemblage 1' and 'Assemblage 2' of early Turonian age. *Wrightoceras* characterizes the basal Turonian of the Algerian Sahara, *Hoplitoides* occurring some distance above (Amard *et al.* 1981: 43–45) and these genera have a similar stratigraphical distribution in Brazil (Bengtson 1983: 44–47). Wiedmann (1960, 1979) describes three Spanish sections containing *Wrightoceras* and *Hoplitoides*. In two of these, at Puentedai and Picofrentes (see Wiedmann 1979: 191–193, text-fig. 15; 207–210, text-fig. 24), the former appears below the latter. At the third, Las Fuentes, however, *Hoplitoides* is listed as occurring, rather incongruously, very close to the bottom of the Turonian (Wiedmann 1979: 205).

This last record notwithstanding, the available evidence indicates that *Wrightoceras* appears very early in the Turonian. *Hoplitoides*, on the other hand, is a younger genus, being most common in the Middle Turonian. Indeed, Kennedy & Wright (1984: 288, 290) found no convincing evidence for its occurrence any earlier. The Nigerian Lower Turonian, however, contains the first members of this genus, as may also be the case in Venezuela.

Hoplitoides latefundatus sp. nov.
Figs 39, 41–4

Compare:
1979 *Hoplitoides* cf. *H. wohltmanni* (von Koenen); Cobban & Hook: 20; pl. 4, figs 3, 4; text-figs 10, 11.
1980 *Hoplitoides* cf. *H. wohltmanni* (von Koenen); Cobban & Hook: 7; pl. 1, figs 3, 4; text-figs 4, 5.

1981 *Hoplitoides wohltmanni* (von Koenen); Cobban & Hook: 30; pl. 5.
1982 *Hoplitoides mirabilis* Pervinquière; Renz: 99; pl. 30, figs 6, 7; pl. 31, fig. 10.

HOLOTYPE. C.90302 (Fig. 42a, b), from the Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria.

PARATYPES. At least fourteen specimens (C.83515, C.85284–5, C.90303–13) from the same horizon and locality as the holotype.

NAME. From the unusually persistent truncation of the venter.

DIAGNOSIS. A smooth *Hoplitoides* retaining a truncated venter until relatively large diameters of 65–75 mm. Venter thereafter sharply rounded.

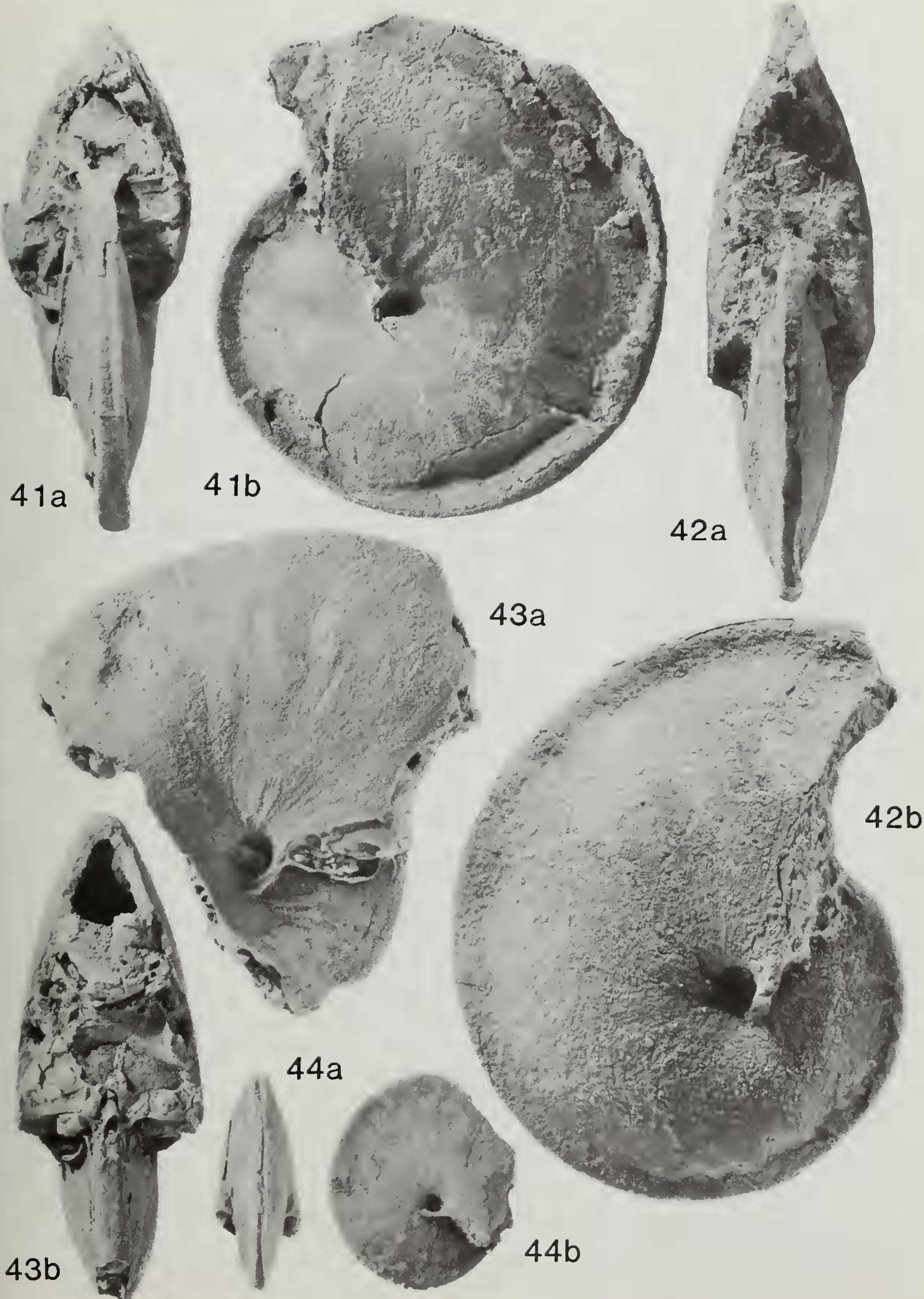
DESCRIPTION. The juvenile whorls are compressed and almost invariably smooth, though rare specimens display faint, broad, prorsiradiate ribs until diameters as large as 45 mm. The juvenile venter is narrow and markedly sulcate until diameters of up to 60 mm, thereafter becoming tabulate and finally, at diameters of 65–75 mm, sharply rounded. The flanks at this stage are usually smooth, though very weak, fold-like ribs may be present in some specimens. The sutures are displayed only in a juvenile specimen (C.85284) of 25 mm diameter; the lateral lobe is broad and deep, the first lateral saddle elongate and rather deeply incised.

Along with this material a mass of large, smooth, involute ammonites were collected. These are all badly crushed and cannot be adequately described. Almost certainly, many represent the outer whorls of this species, indicating maximum diameters in excess of 200 mm.

REMARKS. This material resembles certain previously-described *Hoplitoides* in its lack of pronounced ornament at any growth stage. *H. ingens* (von Koenen) includes one variety, *H. ingens* var. *laevis* Solger (1904: 145; pl. 5, fig. 9), which is virtually smooth and *H. wohltmanni* (von Koenen 1897: pl. 1, fig. 2; pl. 2, figs 3, 9; 1898: 11; pl. 2, figs 1, 4, 7; Solger 1904: 133; pl. 5, fig. 7) possesses at most only a feeble decoration on its inner whorls. Both of these species, however, lose their truncated venters much earlier in ontogeny, at diameters around 20 mm in *H. ingens* (see Solger 1904: 141, 144, 145) and 30 mm in *H. wohltmanni* (see Solger 1904: 136). The material from the early Middle Turonian of New Mexico described as *H.* cf. *H. wohltmanni* by Cobban & Hook (1979, 1980), on the other hand, retains a truncated venter until diameters of at least 65 mm, much longer than in *H. wohltmanni*, as these authors remarked. It closely resembles the present specimens and, though a little younger, it may be conspecific. Another large *Hoplitoides* from New Mexico (Cobban & Hook 1981) does not develop a rounded venter until a diameter of nearly 70 mm and also seems to be closely related. Specimens from Venezuela referred by Renz (1982: 99; pl. 30, figs 6, 7; pl. 31, fig. 10) to *Hoplitoides mirabilis* Pervinquière are further smooth examples showing a comparable ontogenetic development. Pervinquière's species differs in retaining its truncated venter into adulthood and, as indicated above, is better placed in *Wrightoceras*. Egyptian material described by Douvillé (1928: 30; pl. 6, figs 2a, 2b) shows a broad venter at diameters of 60 mm or more and may be related to *H. latefundatus*.

H. gibbosulus (von Koenen) and its varieties (see Solger 1904: pl. 4, fig. 10; text-figs 44–48; Reyment 1955: pl. 17, fig. 8; pl. 18, fig. 1; pl. 19, fig. 4; pl. 21, fig. 3; pl. 22, fig. 2) and *H. crassicostatus* Reyment (1955: pl. 17, figs 3, 4) differ in being strongly ornamented species. *H. koeneni* Solger (1904: pl. 4, figs 8, 9; Reyment 1955: pl. 17, fig. 7; pl. 22, fig. 4) possesses strong ribs on its inner whorls. *H. lacabagnae* Etayo-Serna (1979: 91; pl. 13, fig. 9) and the similar *H. lagiraldae* Etayo-Serna (1979: 92, pl. 13, fig. 14) differ from *H. latefundatus* in that both show pronounced sickle-shaped ribs; in this ornament they resemble the '*H.* aff. *mirabilis* ribbed variety' of Renz (1982: 91; pl. 13, figs 7–9). *H. hernanmojicae* Etayo-Serna (1979: 90; pl. 13, figs 4, 8) is a poorly defined species, but is known to lose its truncated venter early in ontogeny.

Figs 41–44 *Hoplitoides latefundatus* sp. nov. Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Fig. 41a, b, paratype C.90304, × 1. Fig. 42a, b, **holotype** C.90302, × 1. Fig. 43a, b, paratype C.90303, × 1. Fig. 44a, b, paratype C.90309, × 1. See also Fig. 39a, b.


41a
41b
42a
43a
42b
44a
43b
44b

Genus ***HERRICKICERAS*** Cobban & Hook, 1980

TYPE SPECIES. *Placenticeras costatum* Herrick & Johnson, 1900; by monotypy.

***Herrickiceras*? sp.**
Fig. 30a, b

MATERIAL AND OCCURRENCE. A single specimen (C.85287) from the Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria.

REMARKS. Cobban & Hook (1980: 22) proposed the genus *Herrickiceras* for the single species *Placenticeras costatum* Herrick & Johnson (1900: 214; pl. 28, figs 2, 3; Cobban & Hook 1980: 22; pl. 19, figs 10–18; text-fig. 16) from the Middle Turonian of New Mexico. It is characterized by a highly involute, compressed shell with a fairly broad, sulcate, bicarinate venter. There are sinuous ribs which are best developed on the outer part of the flank where they are projected forwards and expanded into clavate ventrolateral tubercles. The Nigerian material, admittedly meagre, shows all these features and may be best referred here. It occurs in the upper part of the Lower Turonian. *Herrickiceras* is otherwise known only from the Rio Puerco Valley area of New Mexico where it occupies a higher stratigraphical position, above the basal Middle Turonian *Collignoniceras woollgari woollgari* Subzone of the western interior.

Stratigraphical conclusions

Owing to the wealth of their ammonite faunas, the Nigerian and Camerounian Turonian have been the subject of considerable biostratigraphic attention (see Fig. 45). Reyment (1954) proposed their first comprehensive, three-fold, subdivision into:

	REYMENT (1954, 1955)	REYMENT (1956, 1965)	BARBER (1957)
UPPER TURONIAN	Youngest Beds	Zone of Romaniceras uchauxiense	Zone of Romaniceras uchauxiense
LOWER TURONIAN	Intermediate Beds	Zone of Hoplitoides ingens (=Zone of Kamerunoceras eschii)	Zone of Kamerunoceras eschii
LOWER TURONIAN	Oldest Beds	Zone of Pseudotissotia (Wrightoceras) wallsi (=Zone of Pachyvascoceras costatum)	Zone of Pseudotissotia (Bauchioceras) nigeriensis Zone of Paravascoceras costatum Zone of Vascoceras bulbosum

	PRESENT WORK	
	N.E. NIGERIA	LOKPANTA AREA
LOWER TURONIAN	Zone of Pseudotissotia nigeriensis (upper extent uncertain)	Zone of Mammites nodosoides beds with Watinoceras
UPPER CENOMANIAN	Zone of Paravascoceras costatum Zone of Vascoceras bulbosum	

Fig. 45 Table showing previous and present proposals for a biostratigraphic subdivision of the Turonian stage in Nigeria and Cameroun. The present work deals only with the Lower Turonian.

1. 'The Oldest Beds', containing the rich vascoceratid faunas characteristic of north-east Nigeria (later described in detail by Barber, 1957) but also represented in less abundance at Ezillo in south-east Nigeria;
2. 'The Intermediate Beds', with *Hoplitoides*, *Mammites*, *Kamerunoceras*, *Benueites*, *Choffaticeras* and *Neoptychites*; and
3. 'The Youngest Beds', with *Hoplitoides* and '*Romaniceras*', occurring in south-west Cameroun only.

Reyment (1955) retained this scheme with little modification though *Watinoceras* was added to the fauna of the 'Intermediate Beds'. Not recognizing a Middle Turonian substage, he regarded the 'Oldest Beds' and 'Intermediate Beds' as Lower Turonian and the 'Youngest Beds' as Upper Turonian. Barber (1957) was able to establish a more detailed zonation of the 'Oldest Beds' at Pindiga in north-east Nigeria, identifying a basal Zone of *Vascoceras bulbosum* (Reyment), a middle Zone of *Paravascoceras costatum* (Reyment) and an upper Zone of *Pseudotissotia* (*Bauchioceras*) *nigeriensis* (Woods). Wozny & Kogbe (1983) found a similar zonation to be applicable at Ashaka Quarry, some 100 km north of Pindiga. In later schemes, Reyment (1956, 1965) termed his 'Oldest Beds' the 'Zone of *Pachyvascoceras costatum* Reyment' (subsequently the 'Zone of *Pseudotissotia* (*Wrightoceras*) *wallsi*'), his 'Intermediate Beds' the 'Zone of *Kamerunoceras eschii*' (subsequently the 'Zone of *Hoplitoides ingens*') and his 'Youngest beds' the 'Zone of *Romaniceras uchauxiense* Collignon', remarking on the ill-defined nature of this last subdivision.

Recent work has shown that the fossiliferous beds in north-east Nigeria described by Barber (1957) are not, in fact, Turonian throughout, but are Upper Cenomanian in their lower part. Barber (1957: 61) himself suspected this, having made a special note of the occurrence of *Metengonoceras dumbli* (Cragin) in the lowest limestone bed exposed at Pindiga. This species is confined to the Cenomanian elsewhere (see, for example, Cobban & Scott 1972; Kennedy, Juignet & Hancock 1981). At Ashaka Quarry both *M. dumbli* and *Euomphaloceras septemseriatum* (Cragin), a reliable late Cenomanian guide fossil, occur in the zone of *Vascoceras bulbosum* in the lower part of the limestone–shale sequence exposed there (Wozny & Kogbe 1983). *E. septemseriatum* is also known from the middle Benue Valley region of Nigeria where it occurs directly below beds with *Paravascoceras*, *Vascoceras*, *Thomasites*, *Pseudotissotia*, *Wrightoceras* and *Neoptychites* (Offodile & Reyment 1976). Though the Upper Cenomanian is, therefore, undoubtedly present in central and north-east Nigeria, the location of its boundary with the Turonian is problematical. The overwhelmingly Tethyan nature of the vascoceratid faunas occurring here precludes ready comparison with the Boreal faunas of areas such as north-west Europe and the western interior of the United States where comprehensive zonal schemes are available and the position of the boundary can be fixed. *Thomasites gongilensis*, however, occurs occasionally in the Upper Cenomanian of the Sergipe Basin, Brazil (Bengtson 1983), and Wright & Kennedy (1981) also recovered examples from the uppermost Cenomanian of southern England. Since this species abounds in the Zone of *Paravascoceras costatum* in north-east Nigeria, Hancock & Kennedy (1981) suggested that the Cenomanian–Turonian boundary might best be placed at the base of the zone of *Pseudotissotia nigeriensis*, thus leaving only this last part of the sequence within the Turonian. As far as southern Nigeria is concerned, Reyment (1978) removed his 'Intermediate Beds' or 'Zone of *Hoplitoides ingens*' fauna from the Lower Turonian, preferring to regard it as early Middle Turonian in age. As a result, only the small fauna from Ezillo listed by Reyment (1955: 98) was assigned to the Lower Turonian. Being composed almost entirely of indigenous species, this fauna defies easy correlation. The extent and faunal character of the Lower Turonian in Nigeria has, therefore, become something of a problem. The present material is thus of great value in reassessing this part of the Nigerian Cretaceous and in suggesting correlation outside the country.

In the western interior of the United States and southern England two zones can be recognized in the Lower Turonian (see Cobban & Scott 1972, Kauffman *et al.* 1978, Cooper 1978, Wright & Kennedy 1981): a basal Zone of *Watinoceras coloradoense*, characterized above all by species of *Watinoceras*; and an upper Zone of *Mammites nodosoides* from which comes the bulk of the described European Lower Turonian ammonites. A similar subdivision seems to be possible in the Lokpanta area of Nigeria (Fig. 45, p. 56). Here, beds dominated by *Watinoceras* spp. can probably be correlated with the zone of *W. coloradoense*. Lying above are beds clearly corresponding with the zone of *M. nodosoides*. They contain the nominal species, *Fagesia* and *Kamerunoceras puebloense*, all characteristic of this zone in the United States western interior (see Cobban & Scott 1972). Below the Turonian beds at Lokpanta, shales have yielded a possible *Metengonoceras* which would indicate the presence of Upper Cenomanian sediments. If confirmed, this occurrence would form an interesting geographical link between beds of this age in north-east Nigeria, the middle Benue Valley and the Calabar region in the extreme south-east of Nigeria (see above, Zaborski 1985).

The fauna from Ezillo described here is more difficult to date precisely. It contains both *Thomasites* and *Wrightoceras*, though the latter occurs a little above the former in north-east Nigeria (Barber 1957, Wozny & Kogbe 1983). Since the entire Ezillo fauna was collected loose from a section several metres thick, however, it is possible that these genera are stratigraphically separated here also. Clearly the affinities of the Ezillo population are with the vascoceratid forms occurring as much as 600 km north in Nigeria, having virtually nothing in common with those at Lokpanta, barely 60 km distant (see Fig. 46). In north-east Nigeria *Thomasites gongilensis* occurs with *Paravascoceras*, another Ezillo faunal element, in beds which, according to Hancock & Kennedy (1981), lie very close to, and possibly just below, the Cenomanian–Turonian boundary. *Wrightoceras wallsi*, on the other hand, is confined to the upper part of the fossiliferous sequences at Pindiga and Ashaka and is of early Turonian age. The ammonite-bearing siltstone at Ezillo described here is underlain by a sequence of shales and oyster-rich limestones exposed on the eastern fringe of Ezillo town in the Western Aboine River (Fig. 1, p. 32). From here Reyment (1955: 65) recorded *Ezilloella ezilloensis* Reyment, a species probably occurring alongside *Euomphaloceras septemseriatum* in the Upper Cenomanian of the middle Benue Valley (Offdile & Reyment 1976). In addition, Offodile & Reyment (1976: 43) reported a possible specimen of *Allocrioceras annulatum* (Shumard) from the Western

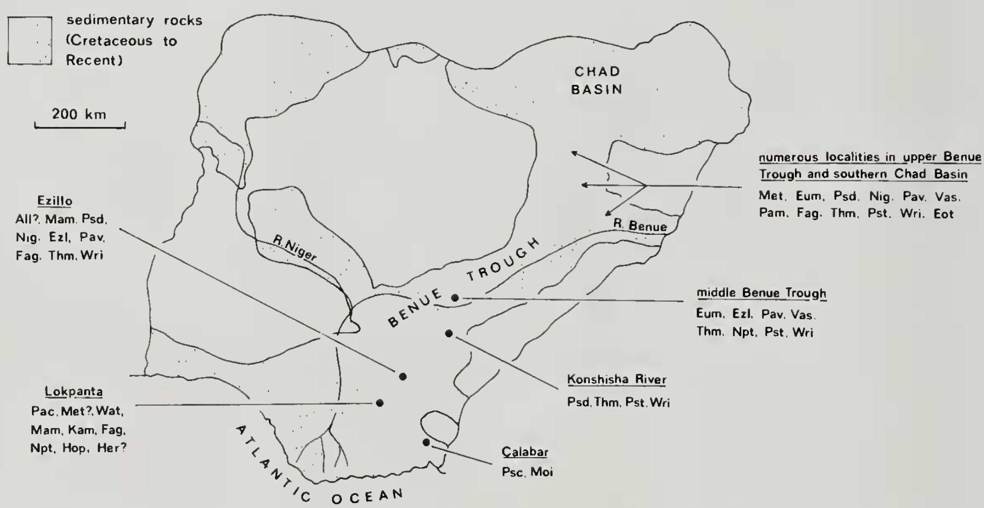


Fig. 46 Map of Nigeria showing distribution of late Cenomanian and early Turonian ammonite genera. All, *Allocrioceras*; Pac, *Pachydesmoceras*; Met, *Metengonoceras*; Psc, *Pseudocalycoceras*; Eum, *Euomphaloceras*; Kam, *Kamerunoceras*; Moi, *Metoicoceras*; Wat, *Watinoceras*; Mam, *Mammites*; Psd, *Pseudaspidoceras*; Nig, *Nigericeras*; Ezl, *Ezilloella*; Pav, *Paravascoceras*; Vas, *Vascoceras*; Pam, *Paramammites*, Fag, *Fagesia*; Thm, *Thomasites*; Npt, *Neoptychites*; Pst, *Pseudotissotia*; Wri, *Wrightoceras*; Eot, *Eotissotia*; Hop, *Hoplitoides*; Her, *Herrickiceras*. Data from Reyment (1954, 1954*a*, 1955), Barber (1957), Offodile & Reyment (1976), Wozny & Kogbe (1983), Zaborski (1985) and original.

Aboine River, another late Cenomanian species of the western interior and elsewhere (Cobban & Scott 1972, Wright & Kennedy 1981: 112). The present Ezillo fauna may therefore be regarded as occurring very close to the Cenomanian–Turonian boundary but almost certainly extending some distance above it. Its direct correlation with the Lokpanta assemblages is, however, not yet possible. Although the fragment of *Mammites*? described from the *Watinoceras*-bearing beds at Lokpanta bears some similarity to *M. dixeyi*, an Ezillo species, there is no useful correspondence between the faunas in these two areas. Only the relatively cosmopolitan genus *Fagesia* otherwise occurs in common.

In the Sergipe Basin, Brazil, *Wrightoceras*, *Thomasites* and *Paravascoceras* occur within a fauna regarded by Bengtson (1983) as basal Turonian ('Turonian 1'). Since, however, *Euomphaloceras septemseriatum* is present also, Bengtson (1983: 43–44) admitted the possibility that the base of the Turonian might be better placed at the bottom of the succeeding ('Turonian 2') faunal assemblage. This part of the Brazilian Turonian contains *Watinoceras amudariense*, *W.* spp., *Neoptychites cephalotus* and *Pachydesmoceras* among others, with *Fagesia* spp. present in the middle part and *Mammites nodosoides* extending throughout its middle and upper parts. This sequence appears to correlate with both the *Watinoceras* and *M. nodosoides*-bearing beds at Lokpanta, although the presence of *Coilopoceras*, *Hoplitoides ingens* and *H. gibbosulus* suggests that the Brazilian beds extend somewhat higher. On the Brazilian evidence, the Ezillo fauna could represent an horizon immediately below the *Watinoceras*-bearing beds at Lokpanta, its absence there being explained by non-exposure of the relevant beds. Alternatively, since uppermost Cenomanian and basal Turonian faunas appear to be present at both Ezillo and Lokpanta, palaeoenvironmental factors would be responsible.

During the late Cenomanian and early Turonian, the Benue Valley and north-eastern part of Nigeria were occupied by an arm of the Tethys extending across the Sahara (see review in Reyment 1980). By late Cenomanian times this epeiric seaway had already flooded the whole of this area. Ammonites such as *Metengonoceras dumbli* and *Euomphaloceras septemseriatum* seem to have been introduced from the widening Atlantic Ocean in the south, the former penetrating as far as Damergou in southern Niger (Schneegans 1943, Greigert & Pougnet 1967: 128). The vascoceratids seem to have been introduced from the north. This vast, shallow seaway, in which similar environmental conditions prevailed over great distances, was overwhelmingly populated by vascoceratid ammonites which have few counterparts in southern Nigeria. The area around Ezillo seems to have been close to the southern limit of this faunal province during the late Cenomanian and early Turonian. The most southerly part of Nigeria was, at this time, probably an area of deeper water, subject to greater influence from open oceanic circulation. Its ammonite faunas show their closest affinities with those of the western interior of the United States. Lower Turonian biofacies show similar variations in Iberia, where mammitids dominate the northern part of Spain, vascoceratids characterizing contemporaneous beds to the south (see Wiedmann 1979: text-fig. 6). Similarly, according to Young & Powell (1978), the Tethyan faunas of Mexico and trans-Pecos Texas are absent from central and northern Texas as a result of environmental factors.

However, perhaps the situation most closely similar to that in Nigeria occurs in Morocco (see Wiedmann *et al.* 1982, Einsele & Wiedmann 1982). The Lower Turonian of the Atlas–Meseta Basin in the north of the country is represented by a limestone facies containing familiar Tethyan genera such as *Vascoceras*, *Paravascoceras*, *Nigericeras* and *Thomasites*. In the west-coastal Tarfaya Basin, on the other hand, a series of laminated bituminous marls with limestone bands and nodules accumulated during the late Cenomanian to early Coniacian. This area lacks both the Turonian vascoceratids and the late Cenomanian *Neolobites*, a widely distributed genus in Tethyan faunas. Instead, the Upper Cenomanian and Turonian are dominated by forms of boreal affinities including *Metoicoceras*, *Watinoceras*, *Mammites*, *Benueites* and *Collignoniceras* (see Collignon 1966). Einsele & Wiedmann (1982) interpreted these faunal differences environmentally, believing the 'black shale' facies of the Tarfaya Basin to have formed in deeper, cooler waters subject to upwelling from the Atlantic Ocean. There is an obvious parallel between the Lower Turonian of Morocco and of Nigeria in both lithofacies and biofacies, but how far the comparison can be taken is, as yet, uncertain. Petters (1978) accounted for Cretaceous black shales in the Benue Trough by envisaging a high influx of organic matter into a relatively shallow seaway.

During the later part of the Turonian the sea retreated from the interior of Nigeria (Reyment 1980) and beds of this age are less easy to identify. Offodile & Reyment (1976), however, recorded Middle Turonian bivalves along with *Collignoniceras*, a diagnostic Middle Turonian ammonite (see Kauffman *et al.* 1978, Cobban & Hook 1979, Kennedy, Wright & Hancock 1980), from Nkalagu in south-east Nigeria. In addition, Reyment (1978) came to regard his 'Zone of *Hoplitoides ingens*' fauna from Wadatta as early Middle Turonian. This fauna is dominated by *Hoplitoides* and *Benueites*, which occur with *Mammites*, *Kamerunoceras* and *Coilopoceras*. Beds of similar age in western Cameroun also contain *Watinoceras*, *Neoptychites* and *Choffaticeras*. In Venezuela, Renz (1982) suggested *Benueites* to be characteristic of the Middle and Upper Turonian and the genus also occupies a relatively high position in the Turonian of the Tarfaya Basin (Collignon 1966). *Hoplitoides* is confined to the Middle Turonian of the western interior, into which *Watinoceras* persists (Cobban & Hook 1979, 1980). *Hoplitoides* does appear somewhat earlier in Nigeria but these are apparently transitional forms with persistently broad venters. Kennedy & Wright (1984) doubted that *Coilopoceras* occurs anywhere earlier than the Middle Turonian. It is probable, therefore, that Reyment (1978) is correct in his Middle Turonian dating of the Wadatta fauna. *Coilopoceras* (= *Glebosoceras* Reyment, 1954) has been recorded from several localities in Nigeria south of the Benue River by Reyment (1954, 1955, 1957) and from the top of the Odukpani Formation near Calabar (Zaborski 1985). In view of Kennedy & Wright's (1984) findings concerning the age of this genus, it is probable that it occurs in Nigeria somewhat higher than the Lower Turonian position previously suggested. Since diagnostic genera of the Upper Turonian such as *Prionocyclus* and *Subprionocyclus* (see Kauffman *et al.* 1978, Wright & Kennedy 1981, Hancock & Kennedy 1981) are unproven in Nigeria, it is not yet possible to identify this substage here with any certainty. Offodile & Reyment (1976: 46) believed the Upper Turonian to be absent in the Nkalagu region, Coniacian beds directly overlying the Middle Turonian.

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